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On the taxonomy of *Heterarthrus* (Hymenoptera, Tenthredinidae), with a review of the West Palaearctic species

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Abstract

The sawfly genus *Heterarthrus* is naturally distributed in the Palaearctic, with a single described Oriental species. Their larvae mine in the leaves of trees and shrubs of Salicaceae, Betulaceae, and Sapindaceae (*Acer*). We here recognise twelve West Palaearctic species as valid, with the status of two additional nominal species group taxa in need of further study: *fruticicolum* Ermolenko, and *smithi* Ermolenko. A key to adults of the species occurring in the West Palaearctic is presented. Two new species are described: *Heterarthus vikbergi* Liston, Mutanen & Viitasaari, **sp. nov.** from females and males reared from leaf-mines in *Populus balsamifera* collected in eastern Finland, and *Heterarthrus fiora* Liston, **sp. nov.** from females reared from *Acer pseudoplatanus*. The latter is a widespread European species, previously misidentified as *Heterarthrus aceris* (Kaltenbach, 1856). New junior subjective synonyms are *Phyllotoma aceris* Kaltenbach, 1856 of *Heterarthrus leucomela* (Klug, 1818), *H. aihinoensis* Haris, 2006 of *H. kamtchaticus* (Malaise, 1931) sp. rev., and *H. imbrosensis* Schedl, 1981 of *H. wuestneii* (Konow, 1905). Lectotypes are designated for *Phyllotoma flavicollis* Gussakovskij, 1947, *P. kamtchatica* Malaise, 1931, and *Tenthredo ochropoda* Klug, 1818.

Keywords

Sawflies, leaf-miners, new species, new synonyms, identification key

Introduction

Twenty-two extant species of *Heterarthrus* were treated as valid by Taeger et al. (2010). These are naturally distributed only in the Old World: mainly in the Palaearctic, with a single described Oriental species, *Heterarthrus birmanus* Malaise, 1961 (Malaise 1961). Two species, *Heterarthrus nemoratus* (Fallén, 1808) and *H. vagans* (Fallén, 1808), have been introduced to North America (Digweed et al. 2009, Humble 2010). Saini and Vasu (1999) wrote that six species occur in the Oriental Realm, citing Benson (1952) as the source of this information, but the latter work contains no such statement.

Heterarthrus larvae are leaf-miners of trees and shrubs of Salicaceae, Betulaceae, and Sapindaceae (*Acer*). Some species have been termed "pests" in various publications, particularly *H. nemoratus* and *H. ochropoda* (Klug, 1818). Although they have seldom been found in Europe to have a major impact on the health or growth of their hosts (Pschorn-Walcher 1982), heavy infestations in regions where they are invasive can cause significant increment losses (Peirson 1929). Also, at high population levels the mines render the affected trees unsightly, thus reducing their aesthetic value in urban environments and gardens (Digweed et al. 2009).

The examination of type specimens and other material, necessary for the identification of a species from Finland, here described as new to science, yielded some additional taxonomic results. These are presented, together with a key to the West Palaearctic species.

Material and methods

Morphological terminology follows Viitasaari (2002). The following abbreviations are used for the names of institutions and collections:

HNHM	Hungarian Natural History Museum, Budapest, Hungary;
MZLU	Lunds universitet, Entomology Collection, Lund, Sweden;
NHRS	Swedish Museum of Natural History, Stockholm, Sweden;
NMS	National Museums of Scotland, Edinburgh, Scotland;
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany;
ZISP	Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia;
ZMHUB	Naturkundemuseum, Berlin, Germany;
ZMUO	Zoological Museum, University of Oulu, Oulu, Finland.

Many specimens of *Heterarthrus* have been sequenced for the mitochondrial COI gene as part of the German Barcode of Life, and the Finnish Barcode of Life projects. The samples were sequenced at the Canadian Centre for DNA Barcoding (CCDB), Ontario, Canada, following the protocols described in deWaard et al. (2008). Partly, the 92 sequences used here were published in Schmidt et al. (2017), available at https://doi.org/10.5883/DS-RSYM, and Kirichenko et al. (2018), available at https://doi.org/10.5883/DS-SALICLM. The nucleotide divergences between the examined specimens and species were calculated with analytical tools in BOLD systems v. 4.0 (http://www.boldsystems.org) and to visualize the divergences between the species a neighbour-joining tree was constructed using the Kimura 2-parameter model in Mega 7.0.21 (Kumar et al. 2016) (Fig. 1). Details of voucher specimens, including voucher data and images, of newly published records are publicly available through the dataset DS-HETER at http://www.boldsystems.org and at https://doi.org/10.5883/DS-HETER.

Results

Character states

The genus-level characters. In the Palaearctic, imagines of *Heterarthrus* are readily distinguished from the other genera of leaf-mining fenusine Blennocampinae by their fully developed fore wing anal cell, with vein 2A+3A complete for its entire length and joined to 1A by an oblique cross-vein (other genera: with vein 2A+3A basally incomplete and either curved up towards 1A to form a small basal loop, or more or less straight). Even in the field, they can usually be recognised by their distinctively shaped head: in dorsal view very wide in proportion to its length, with frontal grooves strongly developed, but frons seldom projecting beyond the anterior of the eyes. Other Fenusini have, in dorsal view, a more globose head: longer relative to its width, with shallower frontal grooves, and the frons usually projects beyond the eyes. Morphologically similar to *Heterarthrus* are *Anheterarthrus* Wei, Nie & Taeger, 2006 species, three of which have been described (Taeger et al. 2010). *Anheterarthrus* is a replacement name for *Anheterus* Wei, 1998 (primary homonym). They are so far known only from Chinese territories in the Oriental Realm. *Anheterarthrus* species differ from *Heterarthrus* species in: claw with weakly developed, obtuse basal lobe (*Heterarthrus* with large, acute basal lobe); inner spur of protibia simple (in *Heterarthrus* with bifid apex); metatibial spur longer than 0.33 × length of metabasitarsus (in *Heterarthrus* at most 0.33 × length of metabasitarsus); in dorsal view length of head of female behind eye longer than length of eye (in *Heterarthrus* length of head of female behind eye shorter than length of eye) (see Wei 1998; the holotypes of all three species were examined by Liston). We obtained COI barcode sequences for two unidentified *Anheterarthrus* specimens, possibly belonging to undescribed species, collected at high altitudes in Yunnan, China (Fig. 1). In a phylogenetic maximum likelihood analysis of available COI data for *Heterarthrus* and *Anheterarthrus*, and in trees rooted to either *Caliroa cerasi* (Linnaeus, 1758) (Blennocampinae: Caliroini) or *Fenusa pumila* Leach, 1817 (Blennocampinae: Fenusini), *Anheterarthrus* is deeply embedded within *Heterarthrus* (results not shown). Since the phylogenetic information content of COI at this phylogenetic level is low, the relationship of these genera requires further study.

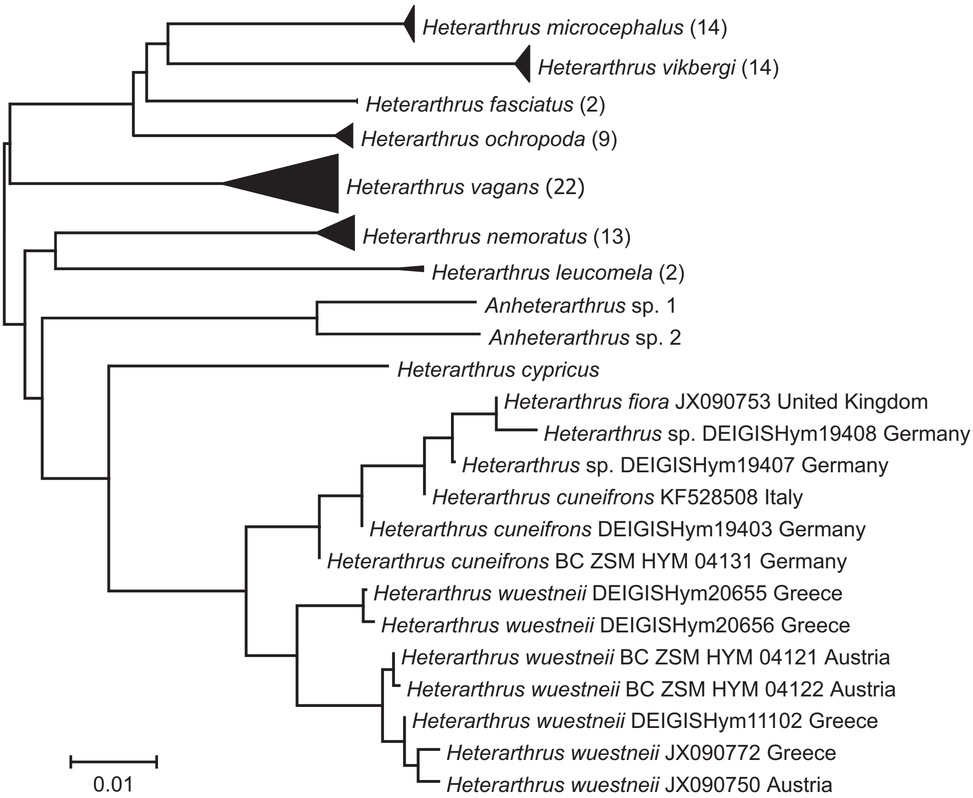
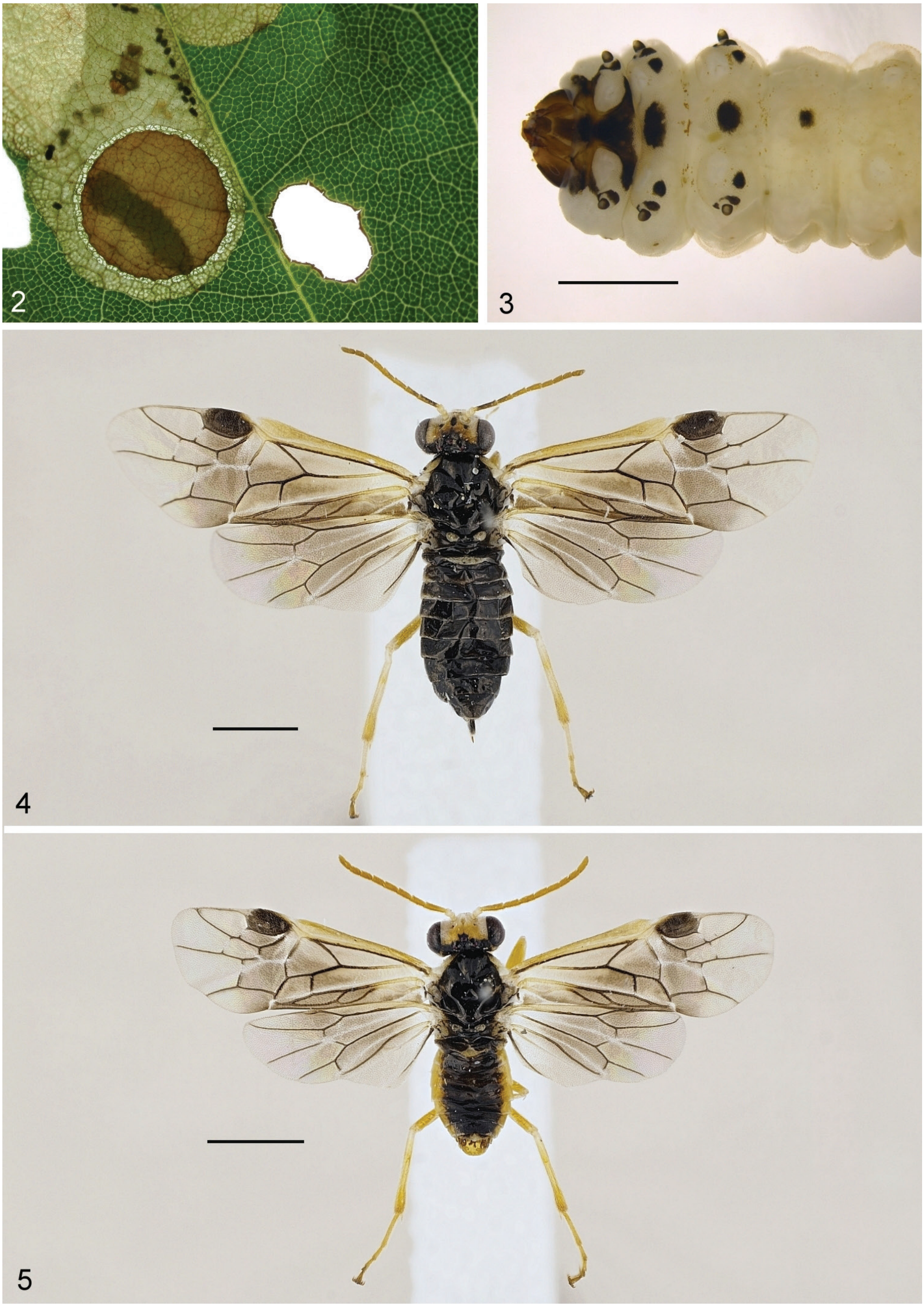


Figure 1. Neighbour-Joining tree of West Palaearctic *Heterarthrus* species based on the barcoding region of the mitochondrial COI gene of 92 specimens of *Heterarthrus* and *Anheterarthrus*. The height of the terminal triangles is proportional to the number of individuals (shown in parentheses), the depth of the triangles to variation within the lineage. For the species feeding on *Acer* spp. each specimen is shown as the species in this complex do not form clearly distinct clusters.

Heterarthrus larvae are distinguishable from those of other leaf-mining Palaearctic sawflies, except some *Profenusa* species, by their strongly reduced thoracic legs: two-segmented in *Heterarthrus*, with claw minute or absent; three- to five-segmented and with well-developed claw in most other Fenusini, and five-segmented with well-developed claw in *Pseudodineura* (Nematinae) (Lorenz and Kraus 1957, Altenhofer 1980a).

Heterarthrus possesses one highly distinctive biological character, apparently not found in any other sawflies: the lens-shaped cocoon is spun inside the leaf and incorporates a circular portion of the upper leaf epidermis (Fig. 2). Other sawflies spin a more or less cylindrical cocoon with rounded ends, or make no cocoon at all, and other leaf-mining sawflies always leave the mine before making a cocoon. Altenhofer (1980b) described the construction of *Heterarthrus* cocoons in considerable detail, and distinguished two different behavioural groups: species in which the cocoon is detached from the leaf before leaf-fall takes place, and species in which the cocoon



Figures 2–5. 2 *Heterarthrus wuestneii* cocoon in mine on *Acer campestre*, Germany, Tübingen, 18.06.2004 (Photo J. Späth) **3** *H. vagans* mature larva, ventral, Sweden, Abisko National Park, 27.08.2018 **4** *H. vikbergi* sp. nov. holotype ♀ **5** *H. vikbergi* sp. nov. paratype ♂. Scale bar: 1mm.

remains within the leaf until after leaf-fall. Only the *Acer*-feeding species (with the exception of *H. leucomela*) have been thought to adopt the former strategy. According to Altenhofer (1980b), the different habits are possibly linked to the risk of desiccation during the cocoon stage, in which the species' phenology also plays a role. The cocoons of "detaching" species can be moved by rapid movements of their inhabitant, so that the cocoon eventually works its way into the upper layer of soil, where it is presumably less at risk of desiccation than in a leaf which is still on the tree. It is noteworthy that among the *Acer*-feeding species, the larva of *H. leucomela* takes much longer to develop than any other species, and so would not have to survive the hottest and driest part of the year in its cocoon which remains in the leaf. However, the differences in behaviour might have resulted from other types of selective pressure, such as predation.

The species-level characters. The external morphological characters used in our key to separate imagines at species level have mostly already been employed in keys or taxonomic treatments of *Heterarthrus* species (e.g. Benson 1952, Altenhofer and Zombori 1987), but the presence or absence of transverse grooves on the anterior part of the median mesoscutal lobes seems first to have been noticed by Hara (2012).

- Coloration. Previous keys to European *Heterarthrus* have all used abdomen colour as the entry character, e.g. Enslin 1914, Benson 1952, Muche 1977, Zhelochovtsev 1988. Although we also found that body colour in most species is stable within rather narrow limits, and that many colour characters are of high diagnostic value, this is not true for *H. vagans*, in which the coloration of the abdomen and head is highly variable. Specimens of this species, particularly males, therefore often key to the wrong species. Wing colour, particularly the colour of the fore wing costa relative to the pterostigma, and sometimes the colour of the wing membranes, is of high diagnostic value in some cases.
- Size of the compound eyes. Species with small eyes have a correspondingly long malar space. The exact points between which the malar space is to be measured are difficult to determine, so that some measurement error is inevitable. On the other hand, interspecific differences in this character are sometimes so great in this genus, that precise measurement is not essential. In some species, the size of the eyes and length of malar space differs significantly between the sexes.
- Shape of the head. In dorsal view the head behind the eyes shows interspecific variability in length and in how strongly it is narrowed towards the posterior. Neither character appears to be directly related to the size of the eyes. A significant practical problem with this character, is that even a slight alteration in viewing angle (i.e. rotation of the head around its transverse axis) greatly affects the perceived proportions (Figs 41, 42).
- Number of antennomeres, and length of antennae. The two characters are partly interdependent, although the presence / absence of a single antennomere in the same species is caused by subdivision, or lack thereof, of the apical flagellomere, and therefore does not affect antenna length. Although the number of antenno-

meres is quite variable in some species, there are sufficient interspecific differences between ranges to make the character useful.

- Median mesoscutal lobes. The transverse grooves on the anterior of the median mesoscutal lobes are strongly developed in all known *Acer*-feeding species except *H. leucomela*, in which they are weak and indistinct. All other West Palaearctic species have very weakly developed grooves, or apparently they are not developed at all, as in most *vagans* specimens.
- Hypopygium. Altenhofer and Zombori (1987) described and illustrated the female hypopygium of four of the *Acer*-feeding species. They indicated that large differences exist, to which they attributed high diagnostic value. We dissected several reared specimens and examined the hypopygia on microscope slides (Figs 22–24), but did not find the differences to be nearly so large as in their illustrations. The paired postero-median structures shown in the drawings by Altenhofer and Zombori (1987, figs 3–5) as discrete "prongs", are in fact more or less weakly sclerotised bands on a transparent, membranous flap, which is extremely delicate and easily destroyed. The shape and extent of the sclerotised parts is very variable. Possibly of some diagnostic value is the outline of the posterior margin of the entire sternum, which in *H. cuneifrons* (Fig. 23) is medially more narrowly and deeply emarginate than in *H. fiora* (Fig. 24) or *H. wuestneii* (Fig. 22), but this needs to be checked in a greater number of specimens. In any case, the differences which we observed are again much smaller than indicated by Altenhofer and Zombori (1987, figs 3–5). In pinned specimens, much apparent variability of the hypopygium, observed *in situ*, is presumably caused by distortion during drying.
- Valvulae 3. Particularly in dorsal view, the profile is often highly distinctive (see Figs 25–28), but in some individuals can be misleading, if the valvulae have been displaced during exposure of the lancet. The length and arrangement of setae on the valvulae are also sometimes helpful, and less prone to alteration by preparation.
- Lancet. The overall shape and structure of the lancet are rather uniform. Nevertheless, diagnostic differences in the shape of the saw teeth are apparent between all West Palaearctic species studied, except for *H. wuestneii* and *H. cuneifrons*.
- Penis valves. More so than the lancet, overall penis valve morphology is fairly uniform across the species studied. At the same time, an unusually high level of intraspecific variability occurs: compare, for example, the two penis valves of *imbrosensis* (= *H. wuestneii*) illustrated by Schedl (1981), and valves of *H. wuestneii* and *H. cuneifrons* as Figs 69–73. It seems very likely that the markedly (compared with most other Tenthredinidae) three-dimensional valves distort greatly during preparation, and that differences in their angle of repose on the microscope slide exacerbate this. The level of apparent intraspecific variability is in our opinion so great, that examination of the penis valve is of little help in identifying specimens of this genus.
- Genetic data. COI mitochondrial barcodes appear to distinguish most species very clearly, with the exception of what might be called the *H. wuestneii* species complex, comprising *H. cuneifrons*, *H. fiora* and *H. wuestneii* (Fig. 1). Thus, species whose imagines are rather easily identified using morphological characters, are also

those which are clearly identifiable by their barcodes. However, barcoding can be generally recommended as a method for the identification of *Heterarthrus* larvae (except the *H. wuestneii* complex), and particularly for the three species feeding on *Populus*, whose larvae are not adequately distinguished morphologically.

– Larvae. West Palaearctic *Heterarthrus* larvae exhibit rather minor interspecific morphological differences. Lorenz and Kraus (1957) describe mainly characters in the shape and arrangement of the dark, sclerotised body markings, and the structure of the anal prolegs. These characters, in conjunction with the identity of the host plant and features of the mine, enable the identification of most species (Altenhofer 1980a, Späth and Liston 2003). For accurate species level identificaton of larvae, barcoding is generally recommended (see above).

Key to West Palaearctic *Heterarthrus* species (imagines)

1 **a** Fore wing costa entirely whitish, much paler than black or dark brown pterostigma (Figs 4, 5, 7, 9) **2**

– **aa** Fore wing costa entirely translucent grey to almost black [or mainly dark with base and apex pale], and pterostigma similarly dark (Figs 29, 32, 37, 38) **5**

2(1) **a** ♀♀ **3**

– **aa** ♂♂. [Antenna: 10–11 antennomeres; completely pale (Figs 5, 56). Upper mesepisternum extensively pale; abdomen laterally and ventrally completely pale (Figs 58, 61, 62)] .... ***Heterarthrus vikbergi*** **Liston, Mutanen & Viitasaari, sp. nov.** ♂

3(2) **a** 10–11 antennomeres (Figs 9, 55); **b** Lateral mesoscutal lobe entirely black (Figs 4, 8); **c** Abdomen laterally with at most a series of posterior white flecks on terga (Figs 9, 51); **d** Mesepisternum mostly black, except at most for a small posterior whitish fleck (Figs 9, 51) **4**

– **aa** 14–17 antennomeres (Fig. 7); **bb** Triangular white marking on interior of lateral mesoscutal lobe (Fig. 6); **cc** Abdomen laterally with contiguous broad white band (Fig. 7); **dd** Upper mesepisternum extensively pale (Fig. 7). [Male unknown. Femora entirely pale (Fig. 7). Body length 4.5–6.8 mm. Hosts: *Populus* spp.] .... ***Heterarthrus fasciatus*** **(Malaise, 1931)** ♀

4(3) **a** Femora basally black; basal halves of coxae black (Fig. 9); **b** Scape and pedicel mostly black (Fig. 9); **c** In dorsal view setae on valvulae 3 longer than combined width of valvulae, and very strongly curved (Fig. 13); **d** Upper outer orbits completely black (Fig. 8). [Male unknown. Body length 4.0–6.0 mm. Hosts: *Betula* species] .... ***Heterarthrus nemoratus*** **(Fallén, 1808)** ♀

– **aa** Femora entirely pale; coxae nearly entirely pale except for extreme base (Fig. 51); **bb** Scape and pedicel whitish (Fig. 55); **cc** In dorsal view setae on valvulae 3 shorter than combined width of valvulae, and not especially curved (Fig. 14); **dd** Upper outer orbits partly pale (orange-brown) (Fig. 53). [Body length 3.0–4.0 mm. Host: *Populus balsamifera* L.] .... ***Heterarthrus vikbergi* Liston, Mutanen & Viitasaari, sp. nov.** ♀

5(1) **a** Basal abdominal terga dull, with dense sculpture (Fig. 15); **b** Median mesoscutal lobes with sculpture at least on anterior (Fig. 17); **c** Median mesoscutal lobes with clear transverse depressions on anterior (Fig. 17); **d** Abdomen mainly black, sometimes with margins of terga and / or sterna finely white **6**

– **aa** Basal abdominal terga shiny, more or less setose, but without sculpture (Fig. 16); **bb** Median mesoscutal lobes either with sculpture throughout, or entirely without sculpture(Fig. 18); **cc** Median mesoscutal lobes without, or with weak, transverse depressions on anterior (Fig. 18); **dd** Abdomen mainly black, sometimes with margins of terga and / or sterna finely white, *or* extensively yellow-red...**10**

6(5) **a** Lower face entirely pale, except for anterior tentorial pits (Fig. 10); **b** Pale parts of head and thorax bright yellow to reddish-yellow (Figs 11, 12); **c** Scape and pedicel sometimes entirely pale or extensively pale (Figs 11, 12) **7**

– **aa** Lower face with at least some larger dark areas (Fig. 40); **bb** Pale parts of head and thorax whitish (Figs 39–41); **cc** Scape and pedicel mostly or entirely black (Fig. 41) **8**

7(6) **a** Outer orbits black (Fig. 12); **b** Female: 11 antennomeres (Fig. 12). [Male: 11 antennomeres] [Host: *Acer platanoides* L.] .... ***Heterarthrus flavicollis* (Gussakovskij, 1947)** ♀♂

– **aa** Outer orbits yellow-orange (Fig. 11); **bb** Female: 12 antennomeres (Fig. 11). [Male: 11–13 antennomeres] [Host: *Acer obtusifolium* Sm.].. ***Heterarthrus cypricus* Schedl, 2005** ♀♂

8(6) **a** ♀♀ **9**

– **aa** ♂♂. [see taxon accounts].. ***Heterarthrus wuestneii* (Konow, 1905), *H. cuneifrons* Altenhofer & Zombori, 1987** ♂

9(8) **a** Serrulae of lancet longer, not so especially protruding (Figs 19, 20). [Tegula from completely white, to completely dark]............................***Heterarthrus wuestneii* (Konow, 1905), *H. cuneifrons* Altenhofer & Zombori, 1987** ♀

– **aa** Serrulae of lancet shorter, more protruding (Fig. 21). [Tegula interior dark, margin pale (Fig. 17)] [Host: *Acer pseudoplatanus* L. Male unknown] .... ***Heterarthrus fiora* Liston, sp. nov.** ♀

10(5) **a** ♀♀ **11**

– **aa** ♂♂..**14**

11(10) **a** Tegula nearly entirely dark; **b** Abdominal terga and sterna partly yellow, or entirely black **12**

– **aa** Tegula entirely pale; **bb** At least abdominal sterna mainly yellow; terga usually also extensively yellow. [Valvulae 3 in dorsal view wide relative to length; longest setae longer than combined width of valvulae, and very strongly curved (Fig. 25). Metafemur entirely yellow, except at most for extreme base. Metatibia mostly yellow. Body length 5.0–6.0 mm]. [Hosts: *Salix* species] ... .***Heterarthrus microcephalus* (Klug, 1818)** ♀

12(11) **a** At most basal half of metafemur darkened (Fig. 30); **b** Metatrochanter and metatrochantellus mainly pale (Fig. 30); **c** Abdomen completely black (Figs 30, 31) to extensively pale (yellow) (Fig. 32)....................................**13**

– **aa** Metafemur black except for extreme apex (whitish) (Fig. 29); **bb** Metatrochanter and metatrochantellus mainly black (Fig. 29); **cc** Abdomen completely black (Fig. 29). [Valvulae 3 in dorsal view rather narrow compared to length, subparallel-sided, with longest setae about as long as combined width of valvulae (Fig. 26). Body length 5.5–7.5 mm] [Hosts: *Acer pseudoplatanus* L. and *campestre* L.] ....***Heterarthrus leucomela*** **(Klug, 1818)** ♀

13(12) **a** Valvulae 3 in dorsal view about as long as broad, more or less dilated apically; longest apical setae longer than combined width of valvulae and strongly curved (Fig. 27); **b** Fore wing membrane basally dark up to about pterostigma, and apically subhyaline (Fig. 31); **c** Median mesoscutellar lobes medioanteriorly finely and densely punctured (Fig. 33); **d** Abdomen black except for whitish hypopygium and sometimes posterior margins of sterna (Figs 30, 31). [Body length 5.0–6.5 mm] [Hosts: *Populus* species].............................. ....***Heterarthrus ochropoda*** **(Klug, 1818)** ♀

– **aa** Valvulae 3 in dorsal view much longer than broad, subparallel-sided; longest apical setae shorter than combined width of valvulae and only slightly curved (Fig. 28); **bb** Fore wing membrane more or less uniformly dark (Fig. 32); **cc** Median mesoscutellar lobes nearly entirely smooth (Fig. 18); **dd** Abdomen *usually* with at least sterna extensively yellow-orange. [Body length 3.0–6.0 mm] [Hosts: *Alnus* species] ....***Heterarthrus vagans*** **(Fallén, 1808)** ♀

14(10) **a** Mesepisternum entirely black; **b** Pedicel mainly black, and *usually* also scape...**15**

– **aa** Upper mesepisternum largely pale; **bb** Pedicel and scape pale...............**16**

15(14) **a** Malar space shorter than diameter of median ocellus (Fig. 35); **b** Median mesoscutellar lobes without sculpture; **c** Abdomen often with extensively pale (yellow-orange) sterna, sometimes also terga. [Body length 2.5–4.5 mm. 11–12 antennomeres. Tegula usually dark, and metafemur yellow-red, at most darkened on basal half: except for 1♂ from Corsica]................................... ....***Heterarthrus vagans*** **(Fallén, 1808)** ♂

– **aa** Malar space about 3 × as long as diameter of median ocellus (Fig. 36); **bb** Median mesoscutellar lobes medioanteriorly finely sculptured. **cc** Abdomen mainly black, with narrow margins of terga and sterna white. [Body length 3.5–6.5 mm. 11–13 antennomeres. Tegula white. Metafemur nearly entirely black]..***Heterarthrus leucomela*** **(Klug, 1818)** ♂

16(14) **a** Fore wing costa mainly dark with base and apex contrastingly pale (Fig. 37); **b** Median mesoscutellar lobes medioanteriorly finely sculptured; **c** Metafemur basally black. [Body length 4.0–5.0 mm. 12–14 antennomeres]........... ....***Heterarthrus ochropoda*** **(Klug, 1818)** ♂

– **aa** Fore wing costa entirely dark (Fig. 38); **bb** Median mesoscutellar lobes without sculpture; **cc** Metafemur entirely pale. [Body length 3.5–4.5 mm. 14–15 antennomeres] ....***Heterarthrus microcephalus*** **(Klug, 1818)** ♂

Taxon accounts and descriptions of new *Heterarthrus* species

Heterarthrus cuneifrons Altenhofer & Zombori, 1987

Heterarthrus cuneifrons Altenhofer & Zombori, 1987: 193–195. Holotype ♀, in HNHM (examined). Type locality: Austria, Lower Austria, Neulengbach.

Material examined. Austria: Lower Austria: 3♀, 2♂ (holotype ♀ and paratypes of *cuneifrons*), Neulengbach, ex larvae *Acer pseudoplatanus*, 05.06.1985 (em. 1986), leg. E. Altenhofer (HNHM).

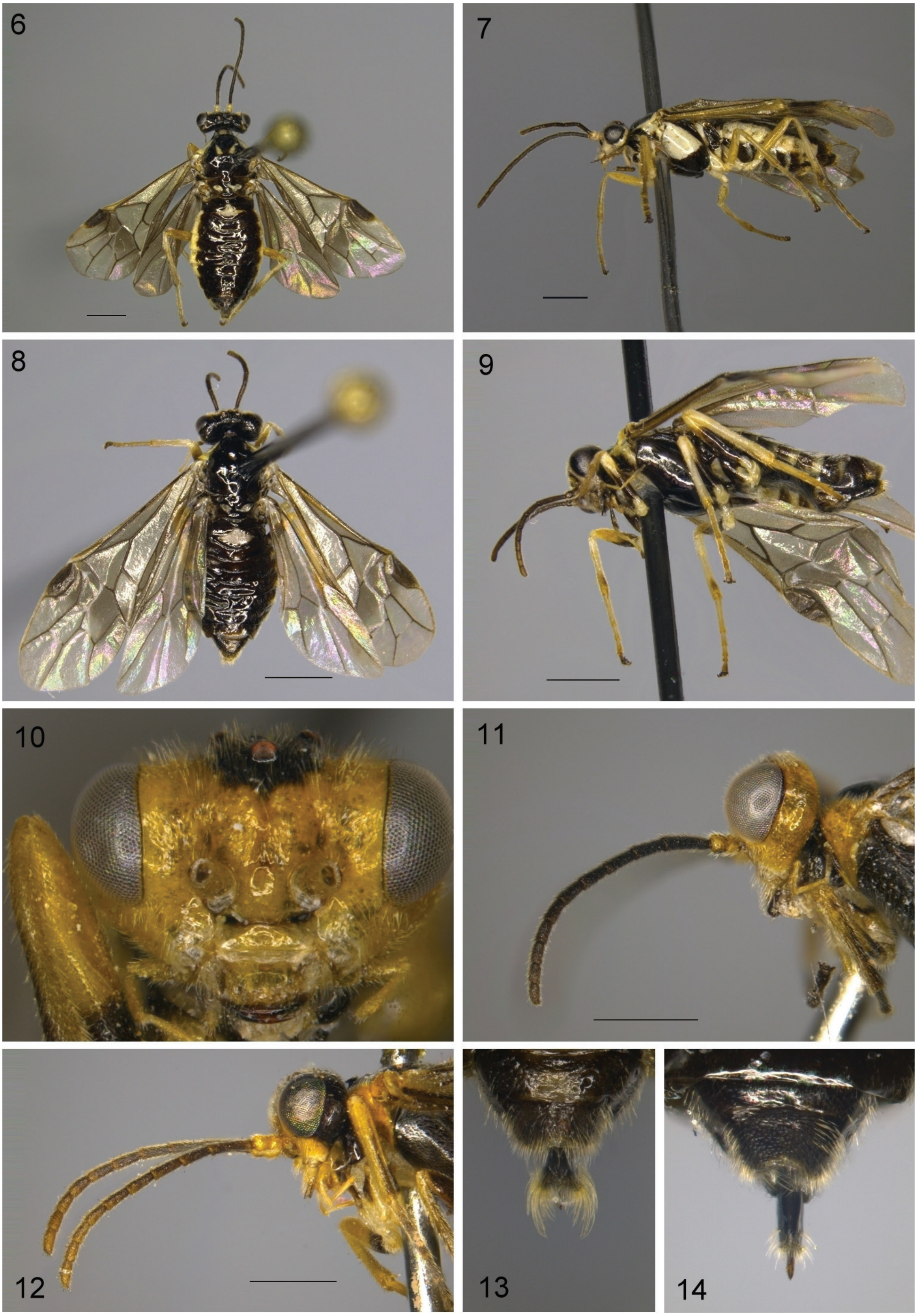
Italy: South Tyrol: 2♀ (DEI-GISHym31979, 31984) 3♂ (DEI-GISHym31988), Salurn, reared *Acer pseudoplatanus*, 07.2000 (em. 04.2001), leg. K. Hellrigl (SDEI).

Remarks. Biologically, *H. cuneifrons* differs from the closely similar *H. wuestneii* and *fiora*, in that it oviposits into the interior of the leaf-blade, whereas the latter oviposit into the margin of the leaf. Furthermore, males of *H. cuneifrons* and *wuestneii* are frequent, but not known in *H. fiora*. *Heterarthrus cuneifrons* and *fiora* have the same host plant species, *Acer pseudoplatanus*, whereas *H. wuestneii* uses different species of *Acer*.

Altenhofer and Zombori (1987) described several morphological characters which they considered to be useful for separating these three species:

- Shape of the sawteeth of the lancet (♀)
- Shape of the hypopygium (♀)
- Shape of the head behind the eyes, in dorsal view (♀)
- Colour of the malar space and tegula (♀)
- Penis valve morphology (♂)

We have already commented (under Character states) on the difficulty of comparing the shape of the head behind the eyes, and on not being able to find the differences in the hypopygium described by Altenhofer and Zombori (1987). In comparing characters between these three nominal species, we relied on reared material from named hosts. Although the sawteeth of *H. fiora* are clearly more prominent than the flatter teeth of *H. cuneifrons* and *wuestneii* (Figs 19–21), we did not find any way of distinguishing the lancets of the latter two from each other. Nor is the colour of the malar space and tegula useful for separating *H. cuneifrons* and *wuestneii*, because of wide variability in *H. wuestneii*. The structure of the lower frons and interantennal area of *H. cuneifrons*, which according to Altenhofer and Zombori (1987) differs greatly from the other two species, appeared to us to be indistinguishable. Perhaps even more so than with head shape, slight changes in viewing angle and illumination have a major effect on the perception of the shape of the raised and depressed parts of the face. Initially, we thought that some correlation might exist between the proportions of the penis valve parts, and the segregates which Altenhofer and Zombori (1987) called *H. cuneifrons* and *healyi* (=*H. wuestneii*). An attempt to quantify this was made by measuring the distance (1) from the tip of the valvura to the highest point on the pseudoceps, and the distance (2) from the highest point on the pseudoceps to the tip of the pseudoceps



Figures 6–14. **6** *Heterarthrus fasciatus* ♀, DEI-GISHym19669 dorsal **7** *H. fasciatus* ♀, DEI-GISHym83889 lateral **8, 9** *H. nemoratus* ♀ DEI-GISHym83888; dorsal, lateral **10, 11** *H. cypricus* ♀ DEI-GISHym83890; head frontal, head and thorax lateral **12** *H. flavicollis* lectotype ♀, head and thorax lateral **13, 14** valvulae 3 dorsal: **13** *H. nemoratus* DEI-GISHym83888 **14** *H. vikbergi* sp. nov. DEI-GISHym83892. Scale bar: 1mm.

(see Fig. 69). The ratios of (1) divided by (2) were 1.32–1.87 in *H. cuneifrons* and 1.37–2.42 in *H. wuestneii* (Table 1).

For the moment, we conclude that *H. cuneifrons* is not distinguishable from *H. wuestneii* using morphological characters or COI barcodes. Nevertheless, the apparent biological differences make us reluctant to synonymise them. Further examination of their status should be made, including analyses of nuclear DNA.

Host plants and biology. *Acer pseudoplatanus* L. is the only recorded host. Oviposition in the middle of the leaf blade, not in the edge. Cocoon falls from leaf before the leaf falls. Univoltine.

Distribution. Central Europe, south to northern Italy, and in southern England (Taeger et al. 2006).

Heterarthrus cypricus Schedl, 2005

Heterarthrus cypricus Schedl, 2005: 137–139. Holotype ♂, in Zoological Museum, University of Amsterdam (not examined). Type locality: Cyprus, Troodos Mountains. Liston and Späth (2008): description of female.

Material examined. Cyprus: 11♀ (including DEI-GISHym83890), 30♂ (SDEI: see Liston and Späth 2008).

Host plants and biology. *Acer obtusifolium* Sm. (Schedl 2005, Liston and Späth 2008). Oviposition in the leaf-edge. Cocoon falls from leaf before the leaf falls. Univoltine.

Distribution. Cyprus (Schedl 2005, Liston and Späth 2008).

Table 1. Proportions of penis valves (see Fig. 69) of the lectotype (male) of *Heterarthrus wuestneii*, reared males of *cuneifrons* and *wuestneii*, and non-reared Greek males of *wuestneii* (1) distance from the tip of the valvura to the highest point on the pseudoceps, and (2) distance from the highest point on the pseudoceps to the distal tip of the pseudoceps (3) ratio of 1 divided by 2. Measured from paper prints of photographic images. Measurements at different scales between specimens.

Species name	Specimen identifier / source of image	Country	Host (reared specimens)	1	2	3 (ratio)
H. wuestneii	DEI-GISHym 3798 Lectotype	Denmark	–	70	51	1.37
	DEI-GISHym 31987	Austria	*Acer campestre*	92	40	2.30
	DEI-GISHym 31987	Austria	*Acer campestre*	92	38	2.42
	DEI-GISHym 31992	Austria	*Acer campestre*	84	45	1.86
	DEI-GISHym 31992	Austria	*Acer campestre*	82	45	1.82
	DEI-GISHym 31993	Austria	*Acer campestre*	99	58	1.71
	DEI-GISHym 31993	Austria	*Acer campestre*	76	49	1.55
	DEI-GISHym 31994	Greece, Peloponnese	–	93	53	1.75
	DEI-GISHym 31994	Greece, Peloponnese	–	87	58	1.50
	Schedl 1981, fig. 3a	Greece, Crete	–	48	29	1.66
	Schedl 1981, fig. 3b	Greece, Crete	–	46	31	1.48
	Liston 2007, fig. 4	Germany	*Acer monspessulanum*	58	30	1.93
	Altenhofer and Zombori 1987, fig. 11	?	*Acer campestre*	48	35	1.37
H. cuneifrons	DEI-GISHym 31988	Italy	*Acer pseudoplatanus*	86	65	1.32
	DEI-GISHym 31988	Italy	*Acer pseudoplatanus*	87	61	1.43
	Altenhofer and Zombori 1987, fig. 12	–	*Acer pseudoplatanus*	71	38	1.87

Heterarthrus fasciatus **(Malaise, 1931)**

Phyllotoma fasciata Malaise, 1931: 28–29. Holotype ♀, in NHRS (not examined). Type locality: Russia, Kamtchatka, Elisowo.

Heterarthrus fasciatus. Hara (2012): holotype of *Phyllotoma fasciata* examined, redescription, hosts, biology, first records from Japan.

Material examined. Japan: Hokkaido: 1♀ (DEI-GISHym19669), Bibai, Koshunai, 43.29950N, 141.84940E, reared *Populus suaveolens*, 16.08.2010 (emergence date), leg. H. Hara (SDEI).

Russia: Tuva Republic: 1♀ (DEI-GISHym83889), East Sayan Mountains, Black Irkut, river shingle and rocks, 1691m, 30.06.2012, leg. W.-H. Liebig (SDEI).

Host plants and biology. Published host plant records are *Populus suaveolens* Fisch. ex Poiteau & A. Vilm. (Hara 2012, Kirichenko et al. 2018) and *P. nigra* L. (Hara 2012). According to the images associated with the reared specimen from the Moscow Region (see below), *Populus balsamifera* L. is also a host. No males have yet been found. The cocoon remains within the leaf. Possibly multivoltine (Hara 2012).

Distribution. The previously known distribution comprises Japan (Hokkaido: Hara 2012), Kamtchatka (Malaise 1931), and East Siberia (Buryat Republic: Sundukov 2017; Novosibirsk and Irkutsk Oblasts: Kirichenko et al. 2018). *Heterarthrus fasciatus* also occurs in European Russia, based on images by Andrej Ponomarev of a reared female. The specimen, misidentified as *H. ochropoda*, is illustrated on the website insecta.pro (insecta.pro/), accessed on 27.03.2019: photos [adult] #68936–68938, [leaf-mines] #68930–68935. The photos are labelled [transliterated]: Moskovskaja obl., Orehovo-Zuevskij r-n, pos. Topolinyj, na topole, with date for one image of leaf-mine 04.07.2014.

Heterarthrus fiora **Liston, sp. nov.**

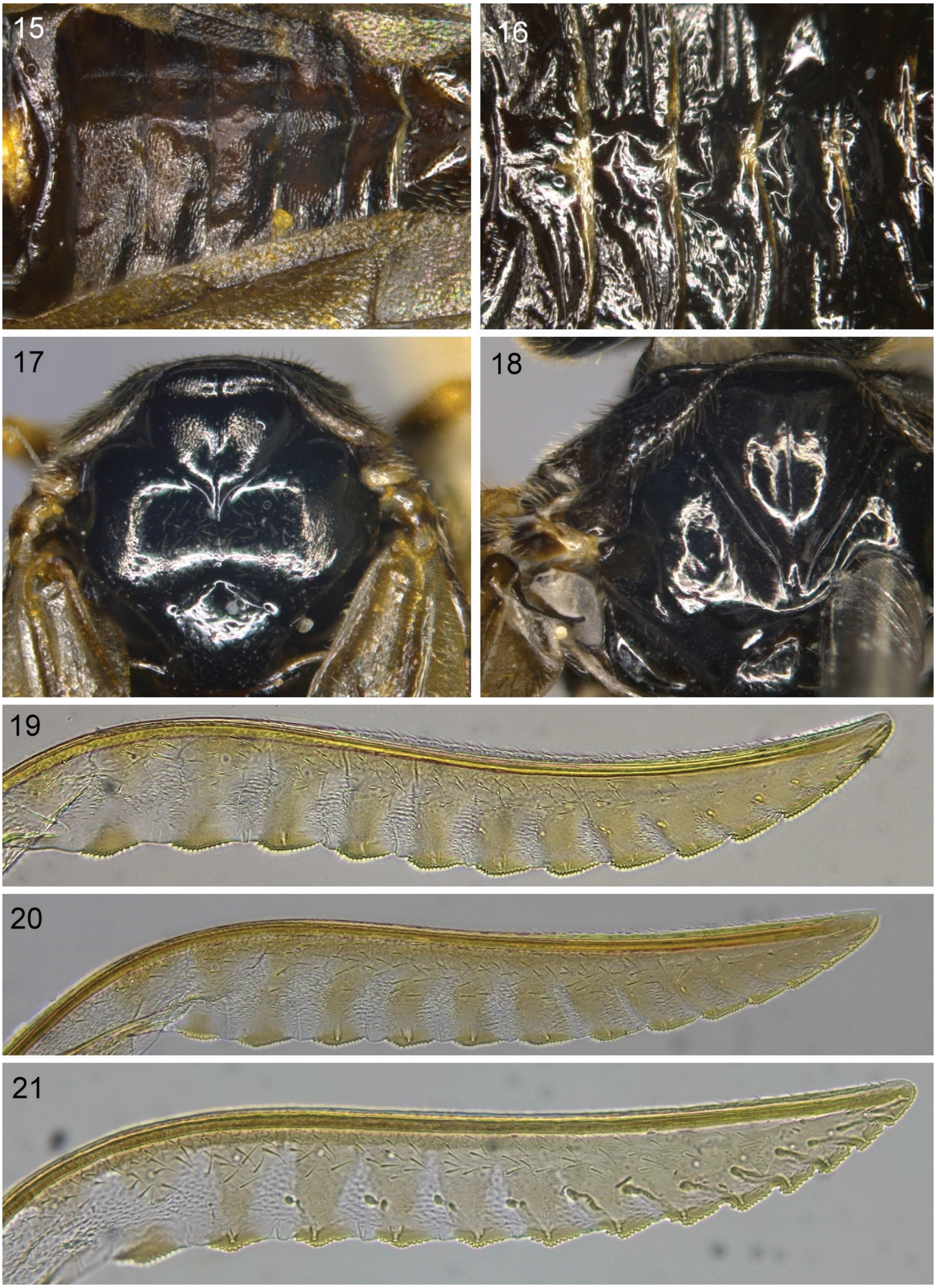
http://zoobank.org/9468A718-FEED-4DD8-AD6E-DE0F7BC6F359

Heterarthrus aceris: misidentification. Altenhofer and Zombori 1987: 188–189, figs 2, 5, 6, 14, 15.

Description. Female (Figs 15, 17, 21, 24, 39–46).

Body length. 3.5–4.5 mm.

Colour. Shiny black and dirty white (Figs 39, 43). Head: black with the following parts pale: labrum, anterior and lateral parts of clypeus, malar space partly, a band along inner orbit about half way up the eye, a U-shaped fleck on supraclypeal area, labial palpomeres 2 and 3, maxillary palpomeres 3 and 4, base of mandible (Fig. 40). Antenna black with 2–3 apical flagellomeres more or less red-brown (Fig. 46). Thorax: black with the following parts white: very narrow lateral and hind margin of prono-



Figures 15–21. *Heterarthrus* ♀ **15, 16** basal abdominal terga: **15** *H. fiora* sp. nov. holotype **16** *H. leucomela* DEI-GISHym31980 **17, 18** median mesoscutal lobes: **17** *H. fiora* sp. nov. DEI-GISHym31976 **18** *H. vagans* DEI-GISHym83893 **19–21** lancets: **19** *H. wuestneii* DEI-GISHym31983 **20** *H. cuneifrons* DEI-GISHym31979 **21** *H. fiora* sp. nov. DEI-GISHym31976.

tum, margins of tegula (Fig. 17). Legs black; pale are apices of coxae, femora, more or less anterior surfaces of all tibiae. Wings light brownish infuscate, veins and pterostigma dark brown. Abdomen: black. Very narrow posterior edges of terga more or less white. Sterna entirely dark.

Structure. Head: with sparse, silvery pubescence. Frons divided in the middle by a longitudinal depression that is rather broad just below the median ocellus, becoming very narrow ventrally, and ending well before an imaginary line connecting the upper margins of the toruli (Fig. 40). Postocellar area short, medially 1.5 times as long as diameter of an ocellus (Figs 41, 42). Malar space 0.29–0.33 × as long as height of eye. Head in dorsal view strongly contracted behind eyes. Usually 12 antennomeres, rarely 11 (Fig. 46). Ratio of lengths of flagellomeres 1–8 approximately as: 100, 75, 71, 62, 51, 46, 42, 40. Thorax: Median mesoscutal lobes with straight transverse grooves at about 0.25 from anterior; coriaceous sculpture on anterior two-thirds (Fig. 17). Lateral lobes with lateral longitudinal coriaceous band. Mesoscutellum shiny with sparse, weak punctures, mesoscutellar appendage highly polished. Metascutellum transversally wrinkled. Mesopleuron covered with short pubescence and finely punctate, but pectus bare and shiny. Abdomen: Tergum 1 less densely sculptured than 2, and more distinctly shiny. Terga 2–7 with dense sculpture, but slightly shiny (Fig. 15). Apical terga with very weak sculpture basally, otherwise unsculptured. Hypopygium deeply emarginate medially (Fig. 24). Sawsheath in dorsal view subparallel-sided, with apex blunt (Fig. 44). Setae curved and directed backwards. Lancet with 13 teeth. 8–11 denticles per tooth (Fig. 21). Apical teeth, apart from last two, clearly separated from each other.

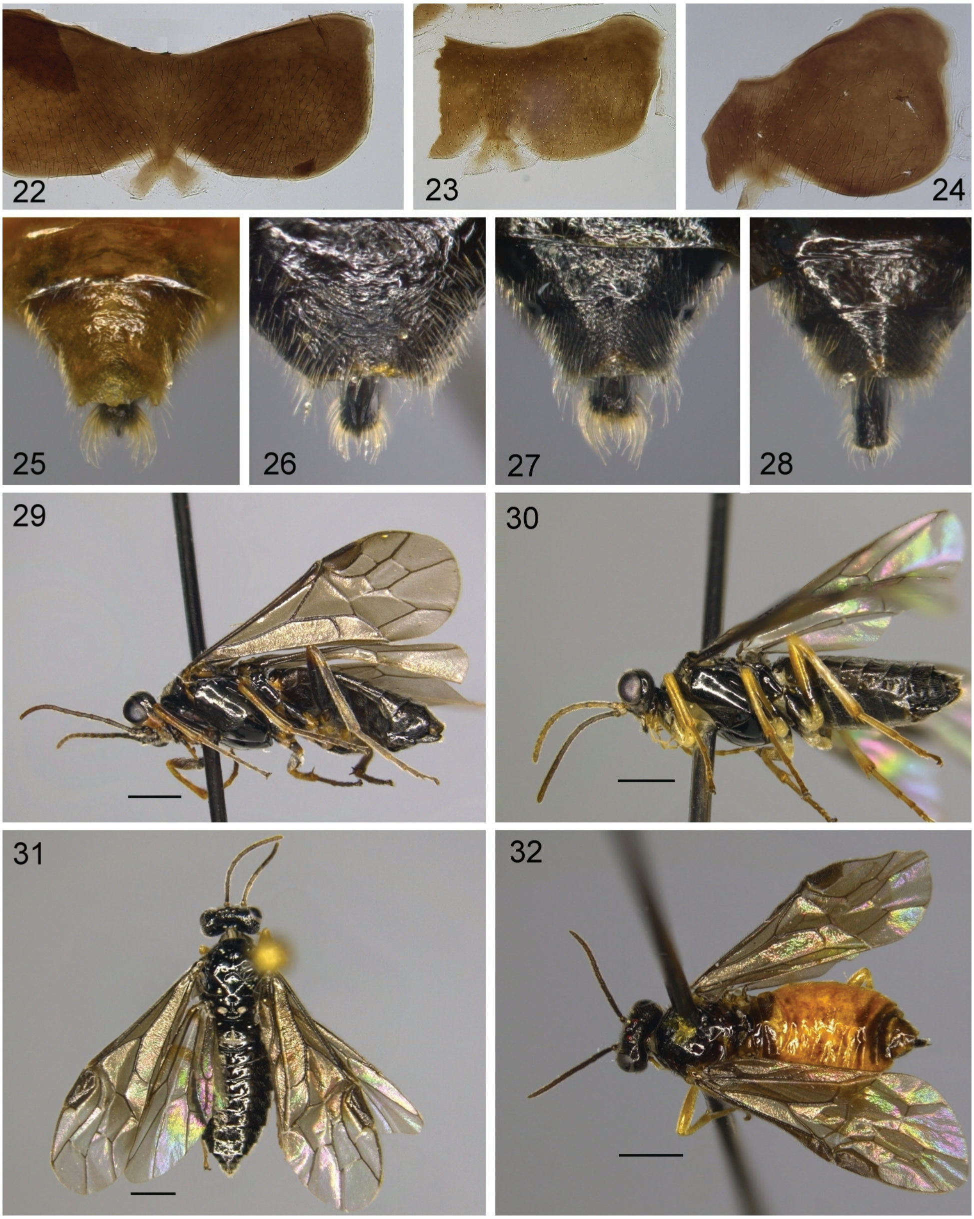
Male. Unknown: the species is exclusively parthenogenetic (Altenhofer and Zombori 1987). Mentions of males under the name *H. aceris* by, for example, Benson (1952) are based on misidentifications of other *Acer*-feeding *Heterarthrus* species (particularly *H. wuestneii* and *H. cuneifrons*) which resemble *H. fiora*.

Variability. Examined specimens are all highly similar, with only very slight differences in the extent of the pale pattern on the head.

***Holotype*:** Female. [Four printed labels:] Austria, Kammern, 12.v.1977, leg. Altenhofer. Larva ex *Acer pseudoplatanus* 8.vii.1976. *Heterarthrus aceris* Kalt. det. Zombori 1977. DEI-GISHym31975. Deposited in HNHM.

***Paratypes*:** Austria: 7♀ (including DEI-GISHym31976, 31977, 83900) same collection data as holotype, but only one specimen with label indicating that it was determined as *H. aceris* by L. Zombori. Deposited in HNHM, except for one specimen, without head, in SDEI. Ireland: 1♀, Tyrone, Pomeroy, 27.5.1987, leg. A. Liston (NMS). Scotland: 1♀, Edinburgh, Corstorphine Hill, ovipositing in leaf edge of *Acer pseudoplatanus*, 1.6.1979, leg. A. Liston (NMS).

Diagnosis. Very similar to *Heterarthrus wuestneii* and *cuneifrons* in size, colour, and external morphology. The lancet teeth of *H. fiora* are somewhat angular, each with 8–11 denticles, and the apical teeth, apart from last two, are clearly separated from each other (Fig. 21). The teeth of *H. wuestneii* and *H. cuneifrons* are more rounded, lower, with 12–15 smaller denticles, and the apical teeth are not clearly separated from each other (Figs 19, 20).



Figures 22–32. *Heterarthrus* **22–24** hypopygia: **22** *H. wuestneii* DEI-GISHym20656 **23** *H. cuneifrons* DEI-GISHym31984 **24** *H. fiora* sp. nov. DEI-GISHym31976 **25–28** valvulae 3 dorsal: **25** *H. microcephalus* DEI-GISHym11397 **26** *H. leucomela* DEI-GISHym83894 **27** *H. ochropoda* DEI-GISHym83895 **28** *H. vagans* DEI-GISHym83896 **29** *H. leucomela* ♀ DEI-GISHym83894 lateral **30, 31** *H. ochropoda* ♀ DEI-GISHym83895 lateral, dorsal **32** *H. vagans* ♀ DEI-GISHym83897 dorsal. Scale bar: 1mm.

Note. the key by Altenhofer and Zombori (1987) states that *H. aceris* (=*fiora*) has malar space and entire tegula dirty white, whereas in *H. cuneifrons* the malar space and basal half of tegula black. These characters are in our opinion not reliable: the tegula of

H. fiora is normally dark on the interior and margined with white (as is in fact written in the description of *H. aceris* by Altenhofer and Zombori, 1987), and *H. cuneifrons* may also have a nearly completely pale malar space. According to Altenhofer and Zombori (1987) the head of *H. aceris* auct. is relatively narrowed behind the eyes, like *H. cuneifrons*, but we are not convinced that any interspecific differences in head shape exist.

Etymology. The name, to be treated as a noun, is derived from the Scottish Gaelic *fior-chrainn* (sycamore tree, *Acer pseudoplatanus* L.).

Host plants and biology. *Acer pseudoplatanus* L.: as recorded by Altenhofer and Zombori (1987), and Späth and Liston (2003). The leaf-mine develops from the edge of the leaf. The circular cocoon, constructed in part from the upper leaf epidermis, separates from the leaf and falls to the ground before the leaf falls from the tree. Univoltine.

Distribution. Probably widespread in Europe, but many records under the name *aceris* are unreliable because of nomenclatural and taxonomic confusion.

Heterarthrus flavicollis **(Gussakovskij, 1947)**

Phyllotoma flavicollis Gussakovskij, 1947: 179–181. Syntypes 10♀, 9♂, in ZISP (Lectotype designated below). Type locality: Georgia, Tbilisi.

Type material examined. ***Lectotype*** *Phyllotoma flavicollis*, here designated: ♀ "DEI-GISHym4753", "Tbilisi, 1946, iz min na klena, T. Zhizhilashvili", "Phyllotoma flavicollis, sp. nov. ♀ (typus) Gussakovski det. 1947", "Lectotype Phyllotoma flavicollis Gussakovskij, 1947 designated A. Liston 2010" (ZISP). Paralectotype ♂: "DEI-GISHym4754", same data as lectotype (ZISP). Further paralectotypes in ZISP were not examined.

Other material examined. Sweden: 6♂, Skåne (see Liston 1993).

Remarks. Apart from its darker head, *H. flavicollis* is very similar to *H. cypricus*. The slightly different number of antennomeres given in the key as distinguishing these species needs to be checked in a greater number of specimens.

Host plants and biology. *Acer platanoides* L. (Altenhofer and Zombori 1987). Mine starts near leaf centre (Liston 1995). Cocoon falls from leaf before the leaf falls from tree. Univoltine.

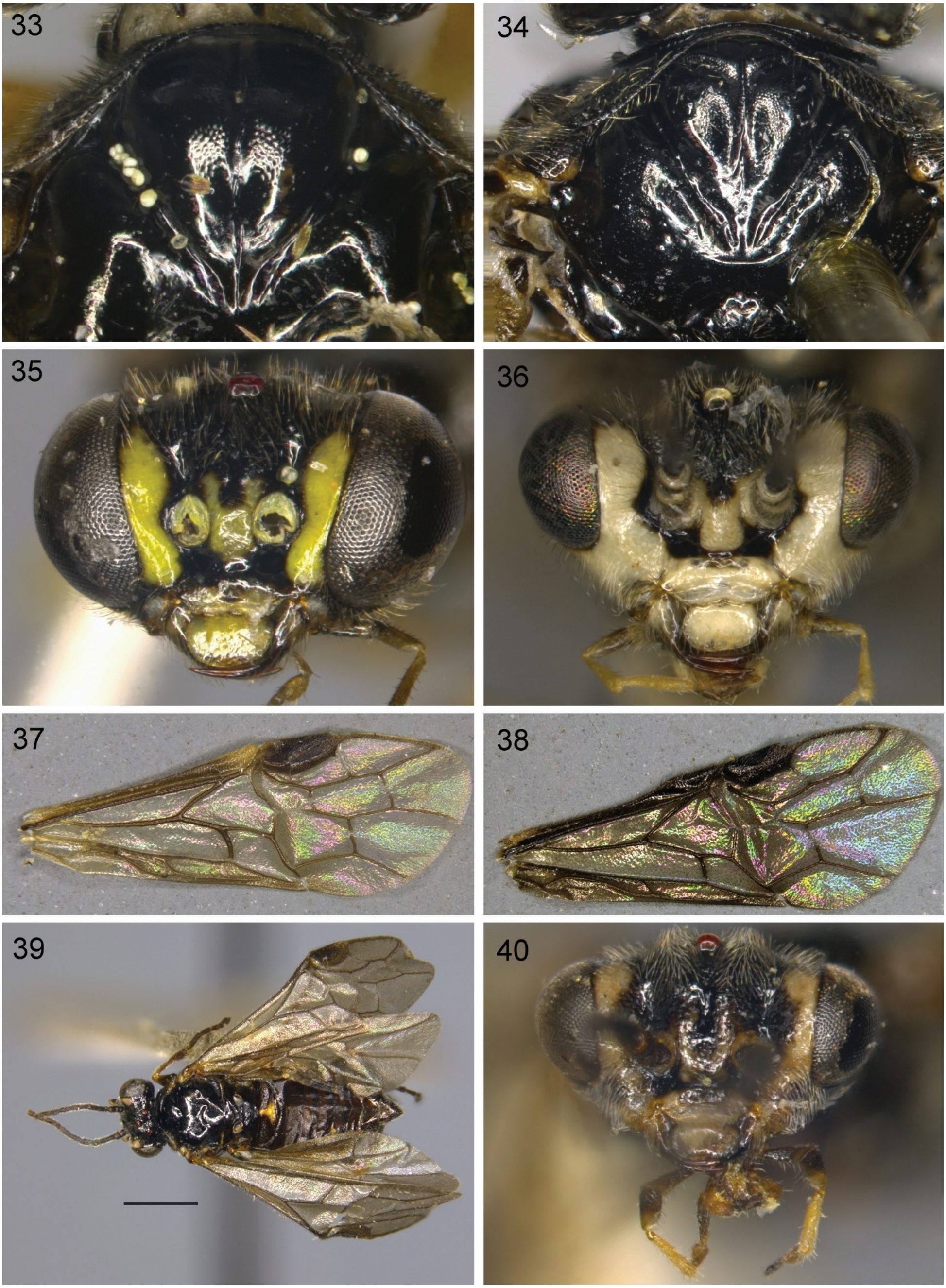
Distribution. Central Europe, north to southern Sweden (Taeger et al. 2006), but rarely recorded, and occurrence apparently very local; Georgia (Gussakovskij 1947).

Heterarthrus fruticicolum **Ermolenko, 1960**

Phyllotoma fruticicolum Ermolenko, 1957: 6–7, 9. Not available. Nomen nudum.

Phyllotoma fruticicolum Ermolenko, 1959: 122, 128. Not available. Nomen nudum.

Heterarthrus fruticicolum Ermolenko, 1960: 207–208. Holotype ♀, Schmalhausen Institute, Kiev (not examined). Type locality: Ukraine, Slavsky District, Khol'sk Pass.



Figures 33–40. *Heterarthrus* **33, 34** median mesoscutal lobes ♀: **33** *H. ochropoda* DEI-GISHym83895 **34** *H. leucomela* DEI-GISHym31980 **35, 36** head frontal ♂: **35** *H. vagans* DEI-GISHym11095 **36** *H. leucomela* DEI-GISHym31981 **37, 38** fore wing ♂: **37** *H. ochropoda* DEI-GISHym83898 **38** *H. microcephalus* DEI-GISHym83899 **39, 40** *H. fiora* sp. nov. ♀ holotype: **39** dorsal **40** head frontal. Scale bar: 1mm.

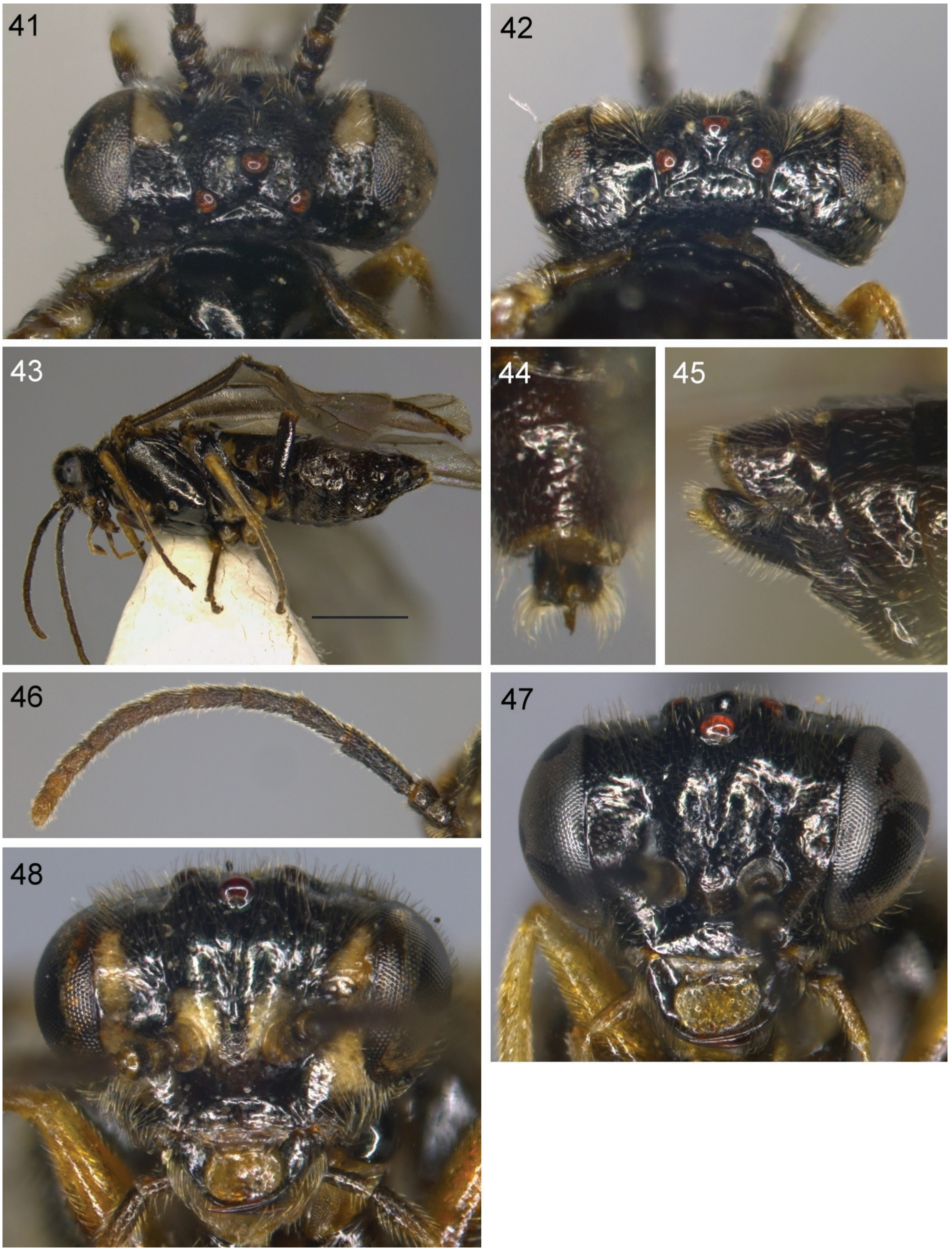
Remarks. The holotype was collected from *Alnus alnobetula* ssp. *alnobetula* (Ehrh.) K. Koch at subalpine levels in the Carpathians. Apart from the single type specimen, only Beneš (2013) has published a record of this taxon: also a single female, from the Giant Mountains (Czech Republic). Although compared in the original description only with *H. ochropoda*, the characters described for *H. fruticicolum* by Ermolenko much more closely resemble *H. vagans*. In fact, in the original description, the only difference seems to be the entirely black body of *H. fruticicolum*. Karel Beneš (personal communication to Liston by electronic mail, 2006) commented on the Czech specimen: "From Ermolenko´s description it is difficult to separate [*H. fruticicolum*] from dark forms of *H. vagans*. However, in *H. fruticicolum* the sheath viewed from above seems to be somewhat broader, slightly wider than hind metatarsus. Antennae are more slender and longer (in my specimen only 9 segments left), scape and pedicel black, apex ventrally piceous. Head width as antennomeres 3 to 8 combined. Segment 8 more than 2 × as long as wide, segment 6 more than 3 × as long as wide. Head pattern as in *H. vagans*, basal segments of maxillar palpi black, thorax including tegulae, and abdomen completely black, only hypopygium brownish. Legs with coxae, trochanters and femora black, only very narrow posterior margins paler; tibiae blackish dorsally, brownish ventrally, tarsi brown. Pterostigma narrower, nearly 3 × as long as wide. Saw seems to have more flat teeth (I saw only several apical teeth protruding from the sheath). This female is very similar to *H. vagans*, [and] maybe only a subalpine race". Two female specimens (SDEI) of *H. vagans* reared by E. Altenhofer from *Alnus alnobetula* ssp. *alnobetula* in subalpine Austria have an extensively pale abdomen, and do not otherwise differ from lowland *H. vagans* specimens reared from other *Alnus* species. The status of *H. fruticicolum* is in need of further study.

Heterarthrus fumipennis (Cameron, 1888), species inquirenda

Phyllotoma fumipennis Cameron, 1888: 218. Syntypes assumed, sex not stated. Type locality: England, Norwich ["taken on alder by Mr. J. B. Bridgman"].

Remarks. It was thought possible that type material might be deposited in the Natural History Museum, London (BMNH), as are most other of Cameron's sawfly types. Gavin Broad and Sue Ryder kindly looked there for possible type material in the Cameron Collection, but found no specimen or record of such which indicated that syntypes of *P. fumipennis* were ever deposited there. Tony Irwin informed Liston (electronic mail of 21.04.2008) that no specimen which can be regarded as a type is amongst the sawflies in the Bridgman Collection housed in the Castle Museum, Norwich, and a search by Darren Mann at the Oxford University Museum of Natural History, where a collection of sawflies bought from Cameron in 1884 is deposited, was also fruitless.

Heterarthrus fumipennis has often been treated as the valid name for a species attached to *Acer campestre*, with *Phyllotoma wuestneii* as a junior synonym (e.g. Enslin 1914, Berland 1947, Zirngiebl 1954, Dadurian 1962, Zombori 1982, Zhelochovtsev 1988), but also as a synonym of *Heterarthrus aceris* (McLachlan, 1867) (Konow 1905b)



Figures 41–48. *Heterarthrus* **41–46** *H. fiora* ♀: **41, 42** head dorsal at different viewing angles, holotype **43** DEI-GISHym83900 lateral **44, 45** DEI-GISHym83900 sawsheath dorsal, lateral **46** DEI-GISHym31977 antenna **47, 48** head frontal ♀: **47** *H. vagans* DEI-GISHym11091 **48** *H. kamtchaticus* (*H. aihinoensis* holotype). Scale bar: 1mm.

or *H. aceris* (Kaltenbach, 1856) (e.g. Lacourt 1999, Taeger et al. 2010). However, as far as we know, none of these authors examined type material of *P. fumipennis*, and the original description does not include any characters which will unequivocally identify it. As occurs repeatedly in descriptions of "new" sawfly species by Cameron, his failure to indicate the sex of his type specimen(s) makes interpretation very difficult. The comment that the specimen (or specimens) was collected from alder [*Alnus*] initially tempts one to think that he could have had before him a specimen of *H. vagans*, but his description of the tegulae as white, and the femora and tibiae extensively dark, contradict this interpretation. The wing colour mentioned by Cameron (1888) was considered by Konow (1905a) and Enslin (1914) to be of value in separating what at that time were presumed to be two European species with similar morphology feeding on maples, but according to present knowledge (Altenhofer and Zombori 1987), wing colour cannot be used to separate any of the now three species of this group known in the British Isles (*H. cuneifrons*, *H. fiora*, and *H. wuestneii*). The apparently completely white tegulae described for *H. fumipennis* would fit either *H. wuestneii* or *cuneifrons*, but not *fiora*. Accordingly, it seems best at present to treat *Phyllotoma fumipennis* as a species inquirenda.

Heterarthrus kamtchaticus (Malaise, 1931), species revocata

Phyllotoma kamtchatica Malaise, 1931: 29. Syntypes ♀, in NHRS (lectotype designated below). Type locality: Russia, Kamtchatka, Elisowo.

Heterarthrus kamtchaticus. Lindqvist (1969): synonymised with *H. vagans* (Fallén, 1808). Ermolenko (1981): treated as valid species, recorded from Kuriles, associated with *Alnus.* Taeger et al. (2010): Listed as synonym of *H. vagans* (Fallén, 1808)

Heterarthrus aihinoensis Haris, 2006: 193. Holotype ♀, in HNHM (examined). Type locality: Russia, Kuriles, Aihino. Syn. nov.

Type material examined. ***Lectotype*** *Phyllotoma kamtchatica*, here designated: ♀ "Kamtschatka Malaise", "E", "Typus", "NHRS-HEVA000001264", "Syntype Phyllotoma kamtchatica Malaise, 1931 teste Taeger & Vardal 2011" (NHRS). Paralectotype: ♀, labels as for lectotype, but: "Paratypus", "NHRS-HEVA000001265" (NHRS).

Holotype *Heterarthrus aihinoensis*: ♀ "Szovjetunió, Kuril-szigetek, Kunasir-sziget, Aihino", 30.vii.1973. leg. Ermolenko", "Holotypus Heterarthrus aihinoensis sp. nov. Haris 2006", "Hungarian Natural History Museum Hymenoptera Coll. Budapest", "DEI-GISHym31973" (HNHM).

Remarks. The coloration of female *Heterarthrus vagans* is highly variable (see under that name). Lindqvist (1969) examined the syntypes of *P. kamtchatica* and concluded that these are indistinguishable from very dark-coloured females of *H. vagans*. He also observed that nearly completely dark-bodied female *H. vagans* occur in Finland, and wrote that [translated from German] "While the abdomen of the nominate form of *H. vagans* is completely or mostly reddish-yellow, in *H. kamtchaticus* this is so extensively black, that at most the base of the venter is slightly pale. All other body parts as well as the wings are similarly darker than in the nominate form". He also examined the lancets of the *P. kamtchatica* types, and found no differences to *H. vagans*. We disagree with parts of his statement: The *P. kamtchatica* types show no trace of pale colour on the basal abdominal sterna, the head has a pale pattern which is as extensive as any examined *H. vagans* females, but slightly differently distributed (Fig. 48), the fore wing is basally smoky up to about the level of the pterostigma and less so at the apex (whereas the fore wing of *vagans* is uniformly smoky), and the tegulae are paler than the rest of thorax (always black in examined *H. vagans*, apart from a specimen from Corsica). Perhaps more significantly, female *H. kamtchaticus* have smaller eyes than *H. vagans*: malar space of *H. kamtchaticus* 0.27–0.33 × height of eye, in *vagans* 0.18–0.22 × height of eye. Furthermore, unlike Lindqvist, we did observe differences between the shape of the lancet sawteeth: in *H. kamtchaticus* they are longer in proportion to their height, the denticles more numerous, with basal denticle smaller and more acute, and the basal and median teeth are less widely separated from each other (compare Fig. 50 with Fig. 49). These differences are significantly greater than the range of infraspecific variability normally encountered in *Heterarthrus*. Probably, these two taxa are indeed closely related. Genetic data, currently lacking for *H. kamtchaticus*, should help to clarify their relationship, but for the present, it seems preferable to treat them as separate species.

Perhaps because its coloration is somewhat similar to female *H. ochropoda*, Haris (2006) compared *H. aihinoensis* to that species, rather than *H. vagans*, although the sawsheath shape of the *H. aihinoensis* holotype strongly resembles the latter. We found only one difference between the *H. aihinoensis* holotype and the *P. kamtchatica* types: the tegulae of the former are slightly paler. This single difference does not seem likely to be significant. Even the colour pattern of their faces is very similar. Accordingly, we propose the synonymy of *H. aihinoensis* and *H. kamtchaticus*.

Host plants and biology. Associated by Ermolenko (1981) with an *Alnus* species, because adults were collected from this.

Distribution. Kamtchatka (Malaise 1931), Kuriles (Ermolenko 1981), and possibly north-east China (Wei 1998).

Heterarthrus leucomela (Klug, 1818)

Tenthredo (*Emphytus*) *leucomela* Klug, 1818: 274. Holotype ♀, in ZMHUB (examined). Type locality: Silesia (now Poland). Note: the name is a noun and therefore not declinable.

Heterarthrus leucomelus (Klug, 1814), misspelling. Altenhofer and Zombori (1987: 186–188): description of adult, larva and biology.

Phyllotoma aceris Kaltenbach, 1856: 257–258. Syntypes (sex not stated), larva, host *Acer pseudoplatanus.* Type material apparently lost. Type locality not stated (but presumably Germany, according to title of the work). New synonym.

Type material examined. Holotype *Tenthredo* (*Emphytus*) *leucomela*: ♀ “Silesia m. Kl.”, “Leucomela Kl”, “14138”, “GBIF-GISHym2425” (ZMHUB).

Other material examined. Austria: Upper Austria: 8♀ 3♂, Linz, larva ex *Acer pseudoplatanus*, 08.1976 (em. 13.5.1977), leg. E. Altenhofer (HNHM). 4♀ 5♂, Linz, larva ex *Acer campestre*, 12.09.1976 (em. 7.5.1977), leg. E. Altenhofer (HNHM). Salz-

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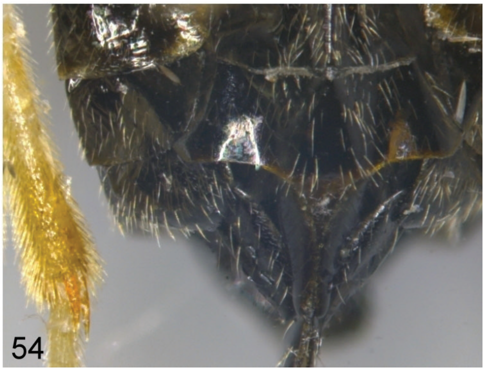


Figures 49–54. *Heterarthrus* **49, 50** lancets: **49** *H. vagans* DEI-GISHym31974 **50** *H. kamtchaticus* HEVA-1264 **51–54** *H. vikbergi* sp. nov. ♀ DEI-GISHym83572: **51** lateral **52** head frontal **53** head dorsal **54** abdomen apex ventral. Scale bar: 1mm.

burg: 2♀, Straßwalchen, larva ex *Acer campestre*, 25.08.1977 (em. 3.05.1978), leg. E. Altenhofer (HNHM). 1♂ (DEI-GISHym31981), Puch bei Hallein, reared *Acer pseudoplatanus*, 02.08.1975, leg. E. Altenhofer (SDEI). Lower Austria: 1♀, Riedenberg, reared ex *Acer campestre*, 08.08.1975 (em. 24.5.1976), leg. E. Altenhofer (private collection M. Viitasaari). 1♀ (DEI-GISHym31980), Etzen, reared ex *Acer pseudoplatanus*, 02.09.1988 (em. 25.04.1989), leg. E. Altenhofer (SDEI).

Germany: Bavaria: 1♀ (DEI-GISHym19032), Dingolfing, Alm, ovipositing in *A. pseudoplatanus* leaf, 15.05.2004, leg. A. Liston (SDEI). Thuringia: 1♀ (DEI-GISHym83894), Luisenthal, 24.05.1986, leg. L. Behne (SDEI).

Remarks. The fate of the type material of *Phyllotoma aceris* Kaltenbach, 1856 is not known. According to Horn et al. (1990), the Kaltenbach Collection was auctioned in London in 1880. The description by Kaltenbach (1856) has in the past been misinterpreted, or overlooked, partly because it appeared in a rare journal which is not available in most libraries. By contrast, the book with the same title, by Kaltenbach (1874), was a widely available and popular work of reference. In Kaltenbach (1874), *P. aceris* is still referred to as a new species. As a result of this, subsequent taxonomists who were unaware of Kaltenbach's 1856 description regarded *Phyllotoma aceris* Kaltenbach, 1874 as a junior homonym (and usually also a synonym) of *Phyllotoma aceris* McLachlan, 1867. All authors of this period assumed that only a single species of *Heterarthrus* occurred on maples. It is important to note that whilst the description of the adult is exactly the same in both Kaltenbach publications, the description of the early stages is more extensive and the biology is described significantly differently in the work of 1874. Either Kaltenbach (1874) had found more material during the intervening years, but failed to recognize that this new material belonged to a species of *Acer*-feeding *Heterarthrus* different to the one which he originally described, or perhaps he revised his text in the light of the observations published by Healy (1867) on the biology of *P. aceris* McLachlan. Altenhofer and Zombori (1987) were sure that the latter explanation is correct. Whatever the reason for the differences between the two Kaltenbach descriptions, only the first description published in 1856 is relevant when considering the identity of *P. aceris* Kaltenbach. The text in Kaltenbach (1856) reads (translated from German):

"*Phyllotoma* (*Emphytus* not *Ericampa* as on p. 176) *Aceris* m. The yellowish larva lives in July and August as a mini-caterpillar in the leaves of sycamore (*Acer pseudoplantanus* [sic!]). It eats out large areas between the two skins of the leaf, which become noticeable as wan [falbe (sic!), probably typographical error for "fahle"], sickly patches on the leaf upperside. To metamorphose, it spins within the mine a circular, flattened cocoon (similar to that of *Tischeria complanella* in oak leaves, and exactly as in *Phyllotoma melanopygus* Klg. and *Phyl. salicis* m. living respectively in the leaves of alder and willow), overwinters as a larva therein and first pupates in the following spring. I obtained the wasp as early as the beginning of May by rearing indoors.

Wasp: black, smooth; antennae 12-membered, towards the apex ringed with brownish; palps whitish, apical member of labial palps black, the thicker basal members of the maxillary palps ringed with black; area of mouth, the inner edge of the green-violet eyes and the tegulae bone-white. Legs black; all knees and the inner sides of the four front legs dirty yellow-white; tarsi brownish to brown. Wings uniformly dark smoky. Length 1.5–2"' [approx. 3.4–4.5 mm. 1 line = approx. 2.25 mm]".

Most significantly, the cocoon of *P. aceris* is stated by Kaltenbach (1856) to remain within the leaf, as is indeed the case with *H. vagans* (Fallén) (= *P. melanopygus* (Klug, 1818)) and *H. microcephalus* (Klug) (= *P. salicis* Kaltenbach, 1856). In the European *Acer*-feeding *Heterarthrus*, cocoons of all species except *H. leucomela* separate from the leaf and fall to the ground soon after they are formed (Altenhofer and Zombori 1987). Healy (1867) describes the latter behaviour for *P. aceris* McLachlan. The relatively late date of collection of Kaltenbach's larvae only fits the slow larval development recorded for *H. leucomela* by Altenhofer and Zombori (1987) and Späth and Liston (2003). All other maple-feeding *Heterarthrus* species finish feeding earlier in the year. Furthermore, only the male of *H. leucomela* has the pattern of black and white colour on the palps (see Altenhofer and Zombori 1987) which Kaltenbach describes for *P. aceris.* The relatively small body size given by Kaltenbach (females of *H. leucomela* are conspicuously larger than other species of *aceris* group) also indicates that the syntypes of *P. aceris* were males: Altenhofer and Zombori (1987: 187) give a body length of 3.5–5.5 mm for male *H. leucomela* and 5.5–7.0 mm for females.

Host plants and biology. *Acer campestre* L. and *A. pseudoplatanus* L. (Altenhofer and Zombori 1987). Oviposition in the leaf edge. The cocoon remains within the leaf. Univoltine.

Distribution. Central and south-east Europe (Taeger et al. 2006).

Heterarthrus microcephalus (Klug, 1818)

Tenthredo (*Emphytus*) *microcephala* Klug, 1818: 274–275. Holotype ♀, in ZMHUB (examined). Type locality: Berlin area ["in hiesiger Gegend"].

Phyllotoma salicis Kaltenbach, 1856: 257. Syntypes, cocoons. Type locality not stated (but presumably Germany, according to title of the work). This name is available according to the International Code of Zoological Nomenclature, Article 12 (Names published before 1931): Kaltenbach's short description of the cocoon constitutes an indication (Article 12.2.8.). New synonym.

Type material examined. Holotype *Tenthredo* (*Emphytus*) *microcephala*: ♀ "Microcephala Kl.", "M. Kl", "14139", GBIF-GISHym2426" (ZMHUB).

Other material examined. FINLAND: 1♀, Kiiminki, 65.10980N, 25.84960E, 7.8.2016, leg. M. Mutanen (ZMUO.029395). 1♀, Linnanmaa, 65.06390N, 25.48070E, 08.08.2016, leg. M. Mutanen (ZMUO.029396).

FRANCE: Ariège: 1♀ (DEI-GISHym11397), Aulus-les-Bains, 08.07.2009, leg. H. Savina (private coll. Savina).

GERMANY: Berlin: 1♂, Berlin, April 1920, leg. M. Hering, (ZMHUB). Brandenburg: 1♂, Königs Wusterhausen, leg. Bischoff (ZMHUB). 1♀, Prötzel, 10.06.2006, leg. Liston

(SDEI). 1♀, Waldsieversdorf, 25.05.2006, leg. Liston (SDEI). Thuringia: 1♀, Apfelstädt, NSG Kleiner See, 27.05.1999, leg. M. Hartmann (Naturkundemuseum Erfurt).

Norway: 1♂, Finnmark, Varanger Peninsula, Båtsfjord, 70.631N, 29.696E, 27.06.2019, leg. Liston & Prous (SDEI).

Sweden: Öland: 1♀, Ölandsleden, 56.523N, 16.571E, 28.05.2013, leg. Liston, M. Prous & A. Taeger (SDEI). Västergötland: 1♂, Sörhamn, 19.06.2013, leg. Liston, M. Prous & A. Taeger (SDEI). Dalarna: 1♀ 1♂ (DEI-GISHym83899), Öje, 11.06.2013, leg. Liston, M. Prous & A. Taeger (SDEI). Jämtland: 1♂, Sveg 24 km E, 18.06.2014, leg. Liston & Prous (SDEI). Torne Lappmark: 1♀, Torneträsk Station, 68.215N, 19.740E, 21.06.2012, leg. Liston & A. Taeger (SDEI).

Remarks. Kaltenbach's (1856) new name, *Phyllotoma salicis*, has apparently been overlooked until now, and was not mentioned in Taeger et al. (2010), or earlier catalogues. The name appears only once in Kaltenbach's series of papers which catalogued the host associations of phytophagous insects in Germany, in the context of the description of *Phyllotoma aceris* Kaltenbach, 1856 (see under *Heterarthrus leucomela*). Later, Kaltenbach apparently realised that his *P. salicis* had already been described, because he refers to the taxon as *Phyllotoma microcephala* Klug (Kaltenbach 1869: 129).

Host plants and biology. numerous *Salix* species (e.g. Buhr 1941). Oviposition in the tip of the leaf. Bivoltine; the second generation more abundant (Altenhofer 2003).

Distribution. Widely distributed in Europe (Taeger et al. 2006), to north of the Arctic circle, the British Isles, and Iberian Peninsula; Transpalaearctic through Armenia, Kyrgystan, Kasachstan, West and East Siberia to the Russian Far East (Sundukov 2017).

Heterarthrus nemoratus (Fallén, 1808)

Hylotoma nemorata Fallén, 1808: 47. Syntypes ♀, possibly in MZLU. Type locality: Vestergöthland [Sweden, Västergötland].

Heterarthrus nemoratus. Taeger et al. (2010: 373): complete synonymy listed.

Material examined. Estonia: 1♀, Vasavere 1.5km E, 04.06.2015, leg. Liston, Prous & Taeger (SDEI).

Finland: 1♀, Liminka 2 km NE, 31.05.2018, leg. Liston & Prous (SDEI).

Germany: Berlin: 1♀, Treptow, 31.05.1906 (ZMHUB). Brandenburg: 1♀, Müncheberg, Gumnitz, 20.05.2011, leg. Liston (SDEI).

Sweden: Dalarna: 1♀ (DEI-GISHym83888), Mora 17km SW, 13.06.2013, leg. Liston, Prous & Taeger (SDEI).

Remarks. The type locality of *Hylotoma nemorata* is not mentioned explicitly by Fallén (1808) on page 47, but the opening sentences of his paper (page 39) state that material collected during a journey to Vestergötland [sic!] comprised the basis of his publication.

Host plants and biology. *Betula* species. In semi-natural habitats in Europe recorded on *Betula pubescens* Ehrh. and *B. pendula* Roth (Pschorn-Walcher and Altenhofer 2000). Many additional species of *Betula* are hosts in European amenity plantings and botanic gardens (Pieronek and Soltyk 1993), and within the non-native range of *H. nemoratus* in North America (Digweed et al. 2009). Oviposition into leaf edge. Cocoon remains in leaf. Entirely parthenogenetic: male unknown. Adults appear late, and larvae develop rather slowly; univoltine (Drouin and Wong 1984).

Distribution. Widespread in northern and central Europe, including the British Isles, but absent in the Iberian Peninsula (Taeger et al. 2006); Armenia, West and East Siberia (Sundukov 2017); introduced to North America where it is present across Canada and adjacent parts of the USA (Digweed et al. 2009).

Heterarthrus ochropoda (Klug, 1818)

Tenthredo (*Emphytus*) *ochropoda* Klug, 1818: 273–274. Syntypes ♀, in ZMHUB (lectotype designated below). Type locality: Germany.

Heterarthrus ochropoda. Taeger et al. (2010: 373): complete synonymy listed.

Type material examined. ***Lectotype*** *Tenthredo* (*Emphytus*) *ochropoda*, here designated: ♀ "Ochropoda Kl.", "M. Kl.", "14137", "GBIF-GISHym2427" (ZMHUB).Paralectotype: same labels as lectotype except "GBIF-GISHym2428" (ZMHUB).

Other material examined. Austria: 1♂ (DEI-GISHym83898), Etzen, 08.1990, em. 18.06.1991, reared *Populus tremula*, leg. E. Altenhofer (SDEI).

Estonia: 3♀ (including DEI-GISHym83589, DEI-GISHym83895), Paadrema 2km NE, 06.06.2015, leg. Liston, Prous & Taeger (SDEI).

France: Ariège: 1♂, Prades, col de Marmore, 9.6.2018, leg. H. Savina (SDEI).

Germany: Bavaria: 1♂, Fürth, leg. E. Enslin (SDEI). Brandenburg: 1♀, Rüdersdorf, 11.05.1919, leg. M. Hering (ZMHUB).

Russia: Khaborovskiy Kray: 1♀, Bikin N 20 km, Boitsovo, Bolshoi Sontsepyok Hill, 26.05.1993, leg. A. Taeger (SDEI).

Sweden: Västmanland: Lindesberg 13km W, 01.06.2013, leg. Liston, Prous & Taeger (SDEI). Dalarna: Lima 33km NW, 10.06.2013, leg. Liston, Prous & Taeger (SDEI).

Host plants and biology. *Populus* species, including *P. tremula* L., *P. alba* L. (Pschorn-Walcher and Altenhofer 2000), *P.* × *canadensis* Moench, *P. deltoides* W. Bartram ex Marshall (Arru 1967), and *P. nigra* L. (Buhr 1941). Has sometimes been stated to cause significant damage to planted poplars (e.g. Arru 1967, Çalmasur and Özbek 2004).

Distribution. Through much of Europe, including the British mainland, but not recorded in the Iberian Peninsula (Taeger et al. 2006); Turkey, Kyrgyzstan, West and East Siberia, Russian Far East (Sundukov 2017).

Heterarthrus smithi Ermolenko, 1994

Heterarthrus smithi Ermolenko, 1994: 17–22. Holotype ♀, in Schmalhausen Institute, Kiev (not examined). Type locality: Azerbaidjan, Talysh, near Lerik village.

Remarks. The type series was collected from *Acer ibericum* M. Bieb., now usually treated as a subspecies of *A. monspessulanum* L. From the original description, *H. smithi* resembles *H. leucomela* in its large size (compared to other *H. aceris* group species), with the body length given as 5.5 mm (♀) and 4.5 mm (♂), and the shape of the serrulae of the lancet illustrated by Ermolenko for *H. smithi* fits well with the illustration for *H. leucomela* by Altenhofer and Zombori (1987). The extensively pale malar space and lower gena, which distinguish female *H. leucomela* from some other *H. aceris* group females, are also shared by *H. smithi*, as are its conspicuously darkened wings. Most of the other characters given by Ermolenko for *H. smithi* do not differ from *H. leucomela*, but are also found in most of the other *Acer*-feeding *Heterarthrus* species. However, the penis valve figure of *H. smithi* by Ermolenko differs considerably from that of *H. leucomela* figured by Altenhofer and Zombori (1987), e. g. the valvura is much more slender in *smithi*. However, we have already expressed our strong doubts on the significance of penis valve characters in *Heterarthrus* (see under Character states, and discussion of *H. cuneifrons*).

Heterarthrus vagans (Fallén, 1808)

Hylotoma vagans Fallén, 1808: 47. Syntypes ♀♂, possibly in MZLU. Type locality: Vestergöthland [Sweden, Västergötland].

Heterarthrus vagans. Taeger et al. (2010: 373): complete synonymy listed; but note that *Phyllotoma kamtchatica* is no longer considered to be conspecific.

Material examined. Austria: Lower Austria: 1♀ (DEI-GISHym31974), no locality, 10.1988, reared *Alnus glutinosa*, em. August 1989, leg. E. Altenhofer (SDEI).

Corsica: 1♂ (DEI-GISHym21130), Haut Ascu, 1493m, 13.06.2013, leg. E. Heibo (private collection E. Heibo).

Cyprus: Paphos District: 1♀ (DEI-GISHym11091), Kidasi, 16.04.2011, leg. Liston (SDEI). 3♂ (DEI-GISHym11184, 11189, 11095), Kidasi, 17.04.2011, leg. Liston (SDEI).

Estonia: Saaremaa: 1♀ (TUZ109299), Abruka, gravel pit, 26.07.2017, leg. V. Soon (Univ. Tartu, Nat. Hist. Mus.).

Germany: Brandenburg: 2♀, Langer Berg im Grumsiner Forst, 3–10.8.1994, leg. DEI Projekt (SDEI). 1♀, Langer Berg im Grumsiner Forst, 26.07–02.08.1995, leg. DEI Projekt (SDEI). 1♂, Langer Berg im Grumsiner Forst, 09.08–16.08.1995, leg. DEI Projekt (SDEI). 1♀, Langer Berg im Grumsiner Forst, 5–12.6.1996, leg. DEI Projekt (SDEI). 1♀ (DEI-GISHym11000), Müncheberg, Gumnitz, 29.05.2010, leg. Liston (SDEI). 1♀ (DEI-GISHym83893), Müncheberg, Gumnitz, 25.05.2008, leg. Liston (SDEI). Thuringia: 2♀, Brandesbachtal bei Netzkater, 27.07–31.05.1996, Malaise trap, leg. A. & M. Taeger (SDEI). 1♀, Brandesbachtal bei Netzkater, 22.07–1.08.1996, Malaise trap, leg. A. & M. Taeger (SDEI).

Italy: Sicily: 1♀ (DEI-GISHym11097), Portella Zilla, ca 9km E Floresta, 18.05.2010, leg. Liston (SDEI).

Portugal: Guarda: 1♂, Seia 9 km W, 400 m, 40.42638N, 7.80716W, 4.5.2012, leg. Blank, Jacobs, Liston & Taeger (SDEI) [first record from Portugal].

Sweden: Torne Lappmark: Abisko National Park, tributary Abisko River, 68.357N, 18.762E, larva in *Alnus incana kolaensis* (Orlova) Á. Löve & D. Löve, 27.08.2018, leg. Liston (SDEI). Abisko National Park, mouth of Abisko River, 68.323N, 18.745E, 5 larvae in *Alnus incana kolaensis*, 28.08.2018, leg. Liston (SDEI).

Remarks. As already noted above, under Character states, the head and abdomen colour of this species is highly variable. In females the abdomen may be almost completely yellow-red, with only tergum 1 and the apical 2–3 terga and sterna more or less dark (Fig. 32). Equally frequent are however females with nearly the entire dorsum of the abdomen dark. According to Lindqvist (1969), the abdomen may sometimes be nearly completely black, with only the basal sterna obscurely paler. We have not, however, ourselves examined such dark females. Male *H. vagans* are generally darker than females, with the dorsum of abdomen usually completely dark, and frequently the whole abdomen dark. In females, the face is usually extensively pale on the inner orbits and interantennal area as in Fig. 35, but sometimes completely black (Fig. 47). The pale colour varies from white, to bright yellow. In both sexes, the coxae and femora are usually completely pale, but occasionally the coxae may be nearly completely black except apically, and up to the basal half of the femora is more or less dark. The thorax is usually entirely black, except for the more or less yellow posteroventral edge of the pronotum, but a male from Corsica (DEI-GISHym21130) has entirely yellow tegulae and the downturned lateral edges of terga 2–6 yellow, with the rest of the abdomen black. This specimen is genetically the most distant from central and northern European, and Canadian *H. vagans*, which have a quite uniform barcode. Only *Alnus alnobetula* subsp. *suaveolens* (Req.) Lambinon & Kerguélen occurs at the Corsican collection locality, so that this can be assumed to be the host. Less distant from the other European and Canadian specimens are specimens from Cyprus and Sicily. See also notes under *H. fruticicolum*, which may only be a dark specimen of *H. vagans*.

Host plants and biology. *Alnus* species, including all the native West European taxa: *A. glutinosa* (L.) Gaertn., *A. incana* (L.) Moench., *A. cordata* (Loisel.) Duby, and *A. alnobetula* ssp. *alnobetula* (Ehrh.) K. Koch (Buhr 1941, Pschorn-Walcher and Altenhofer 2000); also *A. orientalis* Decne. (Liston and Jacobs 2012), *A. rubra* Bong. (Humble 2010), and *A. subcordata* C. A. Mey. (Liston 2011). The cocoon remains in the leaf. Bivoltine; the second generation more abundant (Altenhofer 2003).

Distribution. Widespread in Europe, including the British Isles and Iberian Peninsula (Taeger et al. 2006), from north of the Arctic circle to some of the larger Mediterranean islands; Turkey (Muche 1983); introduced to western North America (British Columbia and Washington; Humble 2010, Looney et al. 2016). According to Sundukov (2017), *H. vagans* has a wide distribution through the East Palaearctic, to the Russian Far East. However, records from at least some of these territories might refer to *H. kamtchaticus*, and voucher specimens therefore require checking.

Heterarthrus vikbergi **Liston, Mutanen & Viitasaari, sp. nov.**

http://zoobank.org/F7AD9636-DD88-4062-9CF9-6254E68E39C5

Description. Female (Figs 4, 14, 51–55, 57).

Body length. 3.0–4.0 mm.

Colour (Figs 4, 51–55). Head (Figs 52–53): mostly pale, shading from yellow-brown dorsally to whitish ventrally. Contiguously dark (black) are occiput, a patch covering postocellar area and frontal field, extending laterally over vertex, and frontally narrowly more or less along antennal furrows to dorsal tentorial maculae. Frontal groove black. Apex of mandible more or less darkened. Apical maxillary and labial palpomeres slightly dark. Antenna (Fig. 55): scape and pedicel whitish; flagellomeres yellowish, 1 and 2 more or less darkened.

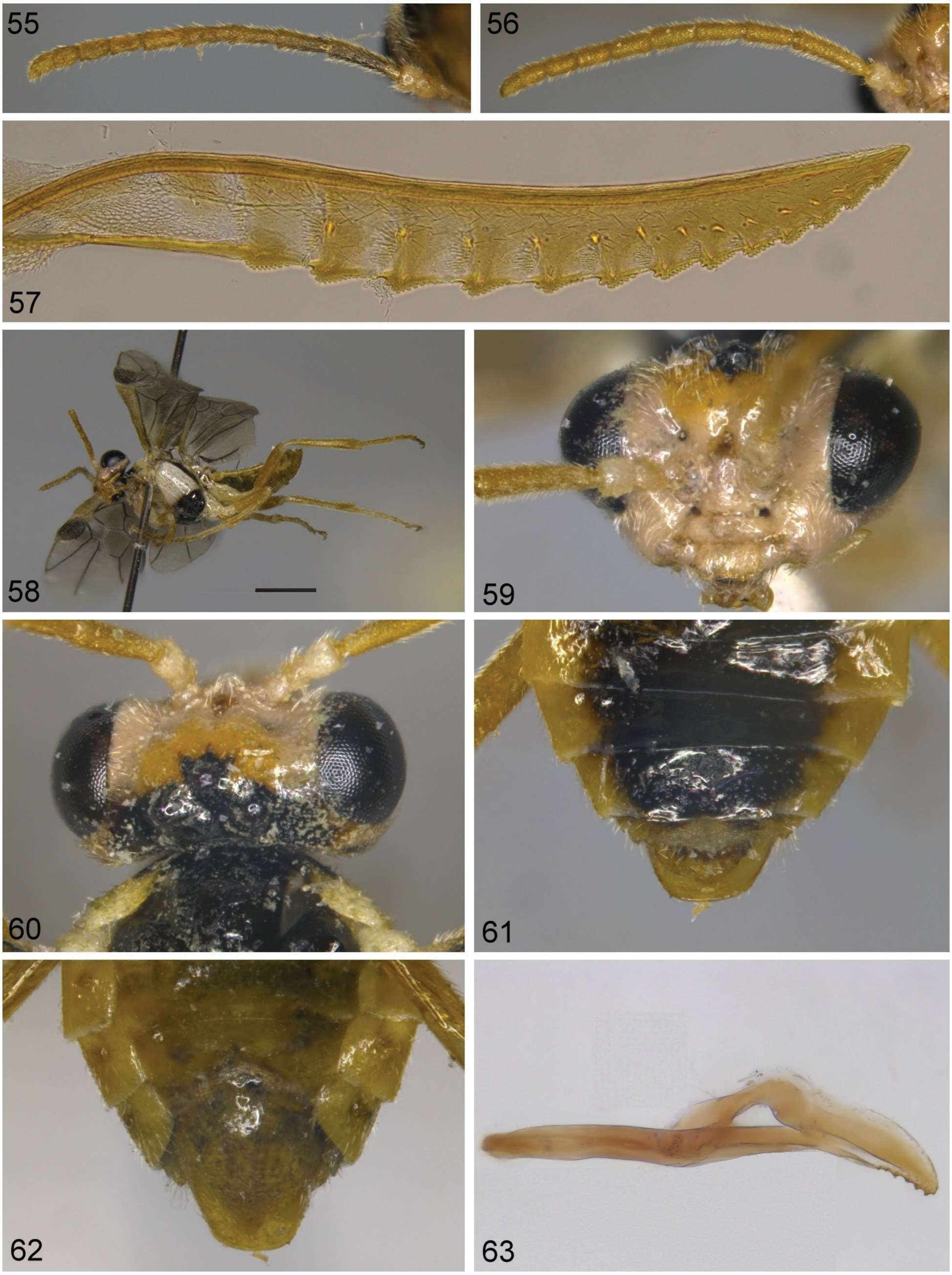
Thorax (Figs 4, 51, 53): black. Whitish are postspiracular sclerite, tegula, broad posterodorsal margins of pronotum, metascutum at least laterally, a fleck on medioposterior of mesepisternum, margins of metepimeron. Legs entirely pale (yellowish), except for very narrowly darkened bases of coxae, and more or less darkened tarsomeres 4 and 5. Wings (Fig. 4): fore wing membrane darkened broadly below pterostigma, and within anal cell, but hyaline distal of apex of pterostigma. Hind wing membrane extensively darkened, but hyaline are apical ca. 0.3, extreme base, and jugal lobe. Venation largely dark. Pale are: C, Sc, small anterior part of fore wing pterostigma basally and apically, all veins in approx. basal 0.25 of fore wing (but R completely dark) and basal 0.2 of hind wing (but 3A completely dark).

Abdomen (Figs 4, 51, 54): black. Obscurely pale are more or less hypopygium (Fig. 54), and margins of downturned parts of terga (Fig. 51).

Structure. Postocellar area about 4 × as broad as long (Fig. 53). Inner margins of eyes in frontal view subparallel (Fig. 52). Antenna: 11–12 antennomeres; about 1.5 × as long as greatest width of head (Fig. 4); pedicel slightly broader than scape. Ratio of lengths of flagellomeres 1–7 approximately as: 100, 62, 58, 58, 51, 44, 42 (Fig. 55). Frontal groove broad, shallow, poorly defined (Fig. 52). Malar space 0.30–0.35 as long as height of compound eye.

Body shiny, without surface sculpture except for sculpture on narrow median part of median mesoscutal lobe. Pubescence pale: length varying from about 0.3 × diameter of median ocellus on upper head, to almost as long as median ocellus on inner orbits, lower head, and mesepisternum. Anterior of median mesoscutal lobe without transverse depressions (Fig. 53). Dorsum of thorax almost entirely glabrous, with only a few minute setae on mesoscutum and posterior of mesoscutellum. Upper ca. 0.6 of mesepisternum densely and evenly setose, lower 0.4 entirely glabrous.

Metatarsomere 1 about as long as combined lengths of following tarsomeres. Inner tooth of tarsal claw about as high as basal lobe and 0.6–0.7 as long as outer; teeth very close together; basal lobe well-developed, acute. Metatibial spurs slightly shorter than apical width of metatibia.



Figures 55–63. *Heterarthrus vikbergi* sp. nov. **55** ♀ DEI-GISHym83572 antenna **56** ♂ DEI-GISHym83573 antenna **57** DEI-GISHym31972 lancet **58–63** ♂ DEI-GISHym83573: **58** lateral **59** head frontal **60** head dorsal **61** abdomen apex dorsal **62** abdomen apex ventral **63** penis valve. Scale bar: 1mm.

Terga 1–8 unsculptured, with sparse, extremely short setae. Terga 9–10 dull, with distally increasingly dense sculpture, and longer setae. Valvulae 3 (Fig. 14) in dorsal view parallel-sided, at least 3 × as long as basal width, apically densely setose; all setae shorter than width of sheath. Lancet (Fig. 57) with 13–14 sawteeth. Each tooth with 6–10 small denticles. Compact groups of ctenidia on venter of lancet above saw teeth 9–10, occupying more than half the length of the basal 2 annular sutures, but proximally the groups become progressively smaller.

Male (Figs 5, 56, 58–63).

Body length. 3.0–3.5 mm.

Colour (Figs 5, 58–62). Head and ventro-lateral parts of body markedly paler than female.

Head (Figs 59, 60): dark dorsal patch extends only slightly anterior of median ocellus; lower head entirely pale. Antenna (Fig. 56): scape and pedicel white, flagellum yellowish.

Thorax (Figs 5, 58): dorsum black, except for tegula, upper edge of pronotum, lateral part of metascutum. Underside of thorax predominantly pale (whitish) except for extreme anterior of pronotum, more or less edges of propleuron, mesepimeron, flecks on the metapleuron, and underside of mesepisternum. Metascutum entirely dark. Legs entirely pale, except for more or less darkened apical tarsomere of mid and hind leg.

Abdomen (Figs 5, 58, 61, 62): pale, except for a broad, black median stripe on terga 1–8.

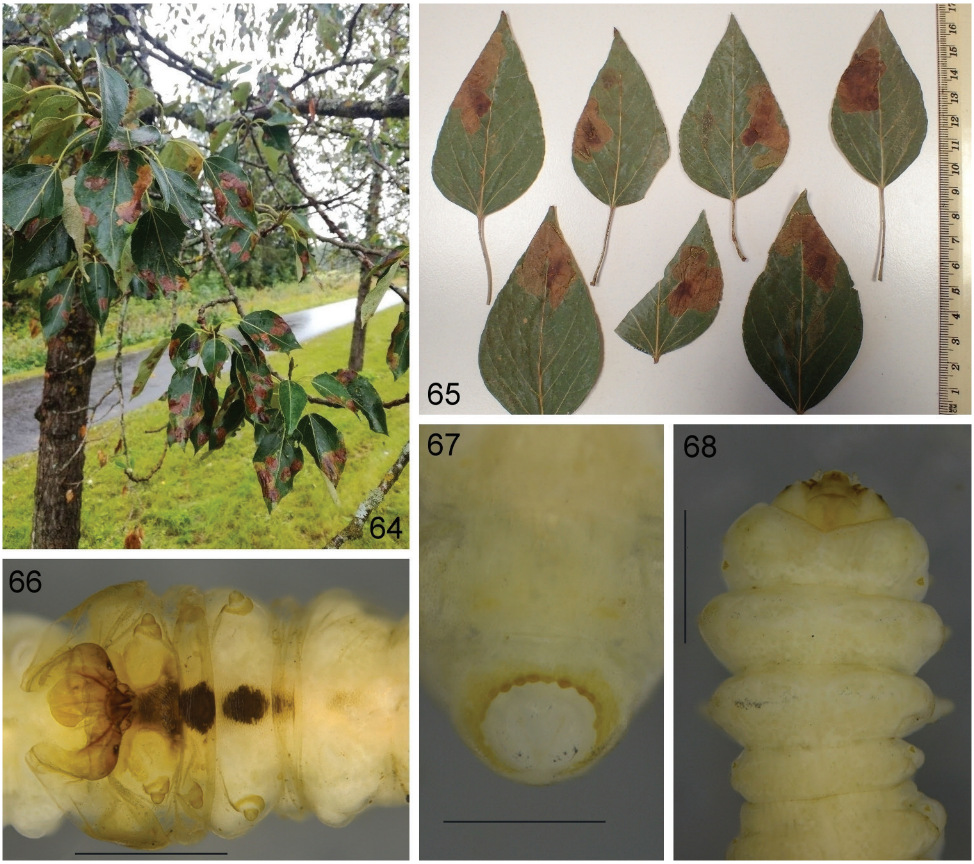
Structure. As female except for: Antenna ca. 1.8–1.9 as long as widest width of head (Fig. 5). Terga 1–5 largely unsculptured, with sparse, extremely short setae. Terga 6–8 dull, with distally increasingly dense sculpture. Penis valve: Fig. 63.

Variability. Female and male. Approximately equal numbers of specimens with 10 or 11 antennomeres: sometimes each antenna of the same specimen appears to have a different number of antennomeres. Relative length proportions of the apical 3 antennomeres highly variable. Fore wing vein 3r-m present or absent, or partly obsolete: frequently unequally developed in each wing of the same specimen. Mesoscutellar appendage black or slightly brown. Female: fleck on medioposterior of mesepisternum variable in size, and sometimes nearly invisible. Lateral part of metascutum always more or less white, but interior from pale brown to black.

Male: usually but not always present is a small pale fleck on anterior of each median mesoscutal lobe, and a pale streak on posterio-lateral edge of lateral lobe.

Larva, full-grown. Length 8–10 mm. Pro-, meso- and metathorax ventrally each with dark median fleck, decreasing in size towards posterior; abdominal sterna one and two also with faint dark markings (Fig. 66). Teeth on sclerotised ring around anal prolegs mostly not clearly separated from each other (Fig. 67).

***Holotype*:** ♀. Finland: Karelia borealis, Tohmajärvi 6906:3673 [Finnish grid: = 62.299N, 30.374E], larva 24.08.2017 on *Populus balsamifera* L., M. Mutanen leg. Deposited in the ZMUO.

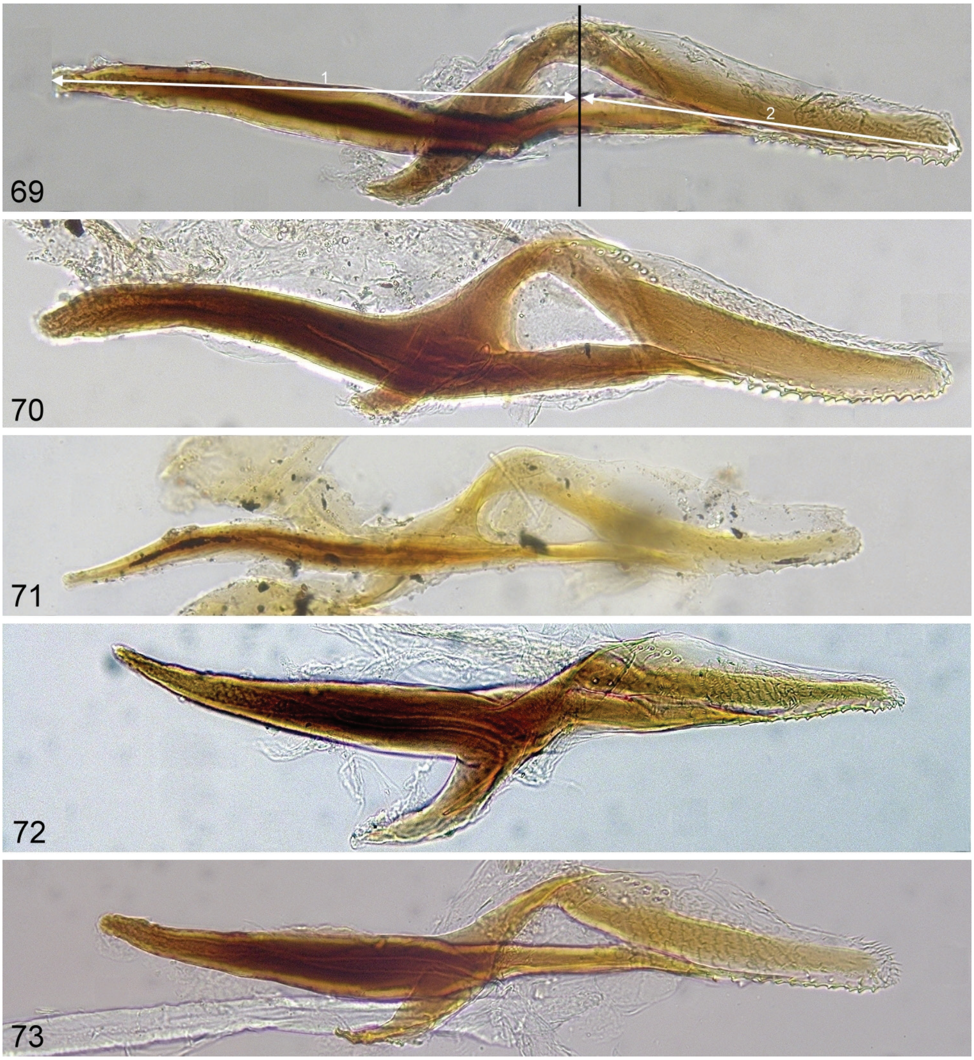


Figures 64–68. *Heterarthrus vikbergi* sp. nov. **64** young *Populus balsamifera* at type locality, with numerous leaf-mines (sawfly mines mixed with mines of *Isochnus sequensi* (Stierlin, 1894): Coleoptera, Curculionidae) **65** pressed *P. balsamifera* leaves containing mines **66** mature larva preserved during moult, ventral **67** mature larva posterior ventral **68** mature larva anterior dorsal. Scale bar: 1mm.

***Paratypes*:** Total: 41♂, 35♀. All same collection data as holotype, except for dates. 5♂, 6♀, larvae collected 26.07.2016. 36♂, 29♀, larvae collected 24.08.2017. Deposited in the Finnish Museum of Natural History, Helsinki, Finland; HNHM; National Museum of Nature and Science, Tsukuba, Japan; NHRS; Private Collection Matti Viitasaari, Helsinki, Finland; Private Collection Veli Vikberg, Janakala, Finland; SDEI; Tartu University Zoological Museum, Tartu, Estonia; United States National Museum, Washington DC, USA; ZMUO.

Other material (immature stages). Two mature larvae (or pronymphs?), collection data as for holotype: DEI-GISHym31985 preserved during ecdysis, with more darkly pigmented cuticle attached (Fig. 66); and DEI-GISHym31986, moulted [weakly pigmented] (Figs 67, 68).

Diagnosis. The female of *H. vikbergi* differs from all other described *Heterarthrus* species in its combination of narrow and proportionately long valvulae 3 in



Figures 69–73. *Heterarthrus* penis valves **69, 70** *H. cuneifrons* DEI-GISHym31988, see *H. cuneifrons* taxon account and Table 1 for details of measurements **71** *H. wuestneii* lectotype **72** *H. wuestneii* DEI-GISHym31987 **73** *H. wuestneii* DEI-GISHym31993.

dorsal view (Fig. 14), the nearly entirely pale fore wing veins C and Sc (which contrast with the otherwise mostly dark venation), and the only partly strongly darkened fore wing membrane (Fig. 4). All other described *Heterarthrus* species have at least the antennal flagellum largely black, whereas male *H. vikbergi* have completely pale antennae (Fig. 56), and females only flagellomeres 1 and 2 more or less dark (Fig. 55). Furthermore, the extensively pale and tricoloured head of *H. vikbergi* is highly distinctive (Figs 52, 59): only the Mediterranean *H. cypricus* Schedl, 2005 has a similarly extensively pale head (but bicoloured: orange and black). For further diagnostic characters of adults, see key to species. Compared to the description of the larva of *H. ochropoda* by Lorenz & Kraus (1957), *H. vikbergi* differs in having a dark marking on venter of abdominal segment 1 (Fig. 66), and the teeth on anal leg ring closer to each other (Fig. 67).

Etymology. The new species is named in honour of Veli Vikberg, whose life-long work on the taxonomy, biology and distribution of sawflies has greatly advanced our understanding of the group.

Host plants and biology. All specimens were reared from leaf-mines on *Populus balsamifera*. Mines were rather abundant on less than ten approximately 20-year old trees, planted in three short rows along the roadside in Tohmajärvi village (Fig. 64). The positions of mines in pressed leaves (Fig. 65) indicate that oviposition is normally in the leaf edge. In this sample, only one mine / larva is present in each leaf. During rearing, many cocoons detached from the leaves, but it is not clear if under natural conditions this takes place before or after leaf-fall. Diameter of 14 cocoons recovered from the rearing pots was 5–7 mm.

Distribution. Only known so far from the type locality, in eastern Finland. The species is unlikely to be indigenous there (see Discussion).

Heterarthrus wuestneii (Konow, 1905)

Phyllotoma aceris McLachlan, 1867: 104. Syntypes ♀ (probably lost). Type locality: not specified [but probably England: see Healy 1867]. Primary homonym of *Phyllotoma aceris* Kaltenbach, 1856 [= *Heterarthrus leucomela* (Klug, 1818)].

Phyllotoma Wüstneii Konow, 1905a: 156. Syntypes ♀, ♂. Lectotype ♂, in SDEI (examined) designated by Muche (1977). Type locality: Denmark, Sonderburg, Insel Alsen.

Heterarthrus imbrosensis W. Schedl, 1981: 151–152. Holotype ♀, in Collection W. Schedl, Innsbruck (examined). Type locality: Greece, Crete, Imbros. **Syn. nov.**

Heterarthrus tauricus Ermolenko, 1984: 53–56. Holotype ♀, in Schmalhausen Institute, Kiev (not examined). Type locality: Ukraine, Crimea, southern slopes of Al-Petri. Synonymy with *wuestneii* suggested by Liston (2007) and adopted by Taeger et al. (2010).

Heterarthrus healyi Altenhofer & Zombori, 1987: 191–193. Replacement name for *Phyllotoma aceris* McLachlan.

Type material examined. *Lectotype* *Phyllotoma Wüstneii*: ♂ “Sonderburg. 12.V.04.”, “Coll. Konow”, “Eberswalde coll. DEI”, “Heterarthrus wüstnei Konow determ. Muche 1976. Mikrosk. Präp. Ty.”, “Type”, “GBIF-GISHym3798”, “Paralectotypus Phyllotoma Wüstneii Konow, 1905 des. Zombori 1980”, “Paralectotypus ♂ Phyllotoma wuestneii Konow, 1905 des. S. M. Blank 2001”, with separate penis valve preparation on glass slide (Symphyta Coll. Nr: 444, SDEI), SDEI. Paralectotypes: 3♀, 1♂ “Sonderburg. 12.V.04.”, and a variety of subsequent labels (SDEI).

Holotype *Heterarthrus imbrosensis*: ♀ “Kreta: Imbros, Nomos Chania, 6.5.1980, leg. W. Schedl”, “Holotypus Heterarthrus imbrosensis Schedl, det. W. Schedl” (Collection W. Schedl, Innsbruck).

Other material examined. Austria: Upper Austria: 3♂ (DEI-GISHym31987, 31992), Linz, larva ex *Acer campestre*, 3.6.1977 (em. 4.5.1978), leg. E. Altenhofer (HNHM). Lower Austria: 1♂ (DEI-GISHym31993), St Pölten, Mine ex *Acer campestre*, 16.6.1976 (em. 20.4.1977), leg. E. Altenhofer (HNHM). 2♀ (DEI-GISHym31983), St Pölten, Mine ex *Acer campestre*, 16.6.1976 (em. 20.4.1977), leg. E. Altenhofer (HNHM). 1♀ (DEI-GISHym31978), St Pölten, *Acer campestre*, 16.6.1976 (em. 28.4.1977), leg. E. Altenhofer (HNHM). 1♀, St Pölten, *Acer campestre*, 16.6.1976 (em. 27.4.1977), leg. E. Altenhofer (HNHM). 1♀ (DEI-GISHym31982), St Pölten, *Acer campestre*, 5.6.1976 (em. 30.4.1977), leg. E. Altenhofer (HNHM).

Germany: Bavaria: 1♀ (DEI-GISHym19407) 3♂ (DEI-GISHym19408), Franconia, Trimberg, reared ex *Acer monspessulanum*, 25.05.2003, leg. Liston (SDEI).

Greece: Peleponnese: 7♀ (DEI-GISHym11102) 2♂, Sparti W 6km, Mistrás, 700 m, 13.04.2008, leg. Liston (SDEI). 1♀, Kalámata SE 15km, Vorio, 650m, 13.04.2008, leg. Liston (SDEI). 4♀ 1♂ (DEI-GISHym31994), Kastanitsa, 25.04.2015, leg. E. Altenhofer (SDEI). 3♀ 2♂, Agios Panteleimonas, 23.04.2015, leg. E. Altenhofer (SDEI). Crete: 5♀ (including DEI-GISHym20656) 7♂ (Liston et al. 2015).

Remarks. Liston et al. (2015) discussed the taxonomy of *H. imbrosensis* and *wuestneii*, pointing out that there is no clear way of separating them morphologically, especially when intermediate specimens from the Peleponnese are taken into account. In any case, the only apparent differences are details of coloration. Greek specimens, especially those from Crete, are usually darker than Central European ones. Neither is the divergence in CO1 barcodes strongly suggestive of the existence of more than one species. Accordingly, we propose the synonymy of *H. imbrosensis* with *H. wuestneii.*

The coloration of *H. wuestneii* varies significantly, even between central European specimens. In females, the malar space can vary from extensively whitish to entirely black, and the supraclypeal area and lower frons may be partly white, or entirely black. The tegula may be entirely white, or only with posterior third whitish.

We have not found any morphological characters which will distinguish *H. wuestneii* from *H. cuneifrons.* According to Altenhofer and Zombori (1987), the structure of the frons should be different, but this was not evident in the specimens which we examined. Variability in penis valve morphology is considerable: see also discussion under *H. cuneifrons*. The form of the penis valve is somewhat different for these species as illustrated by Altenhofer and Zombori (1987, figs 11 and 12). However, the penis valve of the *H. wuestneii* lectotype (Fig. 71) does not fit very well with either of their drawings, and the penis valve of the reared *H. wuestneii* specimen illustrated by Liston (2007, fig. 4) looks different from any of these. The drawing of a penis valve of *H. wuestneii* by Muche (1977), presumably representing the lectotype, which was dissected by Muche and permanently mounted on a glass slide, is very misleading. Only the sclerotised part of the valviceps is outlined; the membranous dorsal part is omitted. We suggest that because of variability, *H. cuneifrons* and *wuestneii* males cannot be distinguished by penis valve morphology.

Host plants and biology. As a result of the synonymy proposed above, *H. wuestneii* is known to use two different host species: *Acer campestre* L. (Altenhofer and Zombori 1987), and *A. sempervirens* (Liston et al. 2015). The records from *A. monspessula-*

num L. (Liston 2007) require confirmation, because the specimens could either belong to *H. wuestneii* or *H. cuneifrons*.

Distribution. Central and southern Europe (Taeger et al. 2006), including some of the larger Mediterranean Islands (Corsica, Sicily, Crete).

Discussion

Four West Palaearctic *Heterarthrus* species are associated with Salicaceae (*H. microcephalus* on *Salix*; *H. fasciatus*, *ochropoda* and *vikbergi* on *Populus*), and two with Betulaceae (*H. nemoratus* on *Betula*; *H. vagans* on *Alnus*). The status of each of these as separate species is supported by clear differences in morphology, DNA barcodes, and for *H. nemoratus* and *vagans* also by host association. Further studies on the morphologically and genetically highly variable *H. vagans* would however be desirable, particularly to include West Palaearctic samples from *Alnus alnobetula*, and forms in the East Palaearctic which are morphologically similar. Species limits of the morphologically and genetically distinctive *Acer*-feeding *Heterarthrus leucomela* also seem unambiguous. Less clear is the taxonomy of the other five West Palaearctic *Acer*-feeding species *H. cuneifrons*, *cypricus*, *fiora*, *flavicollis*, and *wuestneii*, which we here for the meantime treat as valid. Leppänen et al. (2012, fig. 1) indicated that *H. wuestneii* (under the names *healyi* and *imbrosensis*), *fiora* (as *aceris*) and *cuneifrons* are very closely related. However, currently available genetic data for this species complex does not include *H. flavicollis*, and interpretation of data for the other species is difficult because of misidentifications and nomenclatural inconsistency. On the other hand, as summarised in the identification key, morphological differentiation of these taxa is in most cases possible, except for *H. cuneifrons* and *wuestneii*. Unclear is how strongly host plant specificity is correlated with these characters. Previous studies have postulated strict monophagy of most *Acer*-mining *Heterarthrus* species on single *Acer* species (e.g. Altenhofer 1980a, Altenhofer and Zombori 1987), but we suspect that host associations in this group of species are sometimes less strict. A misleading impression has possibly arisen, because older data on host plant associations are nearly all from central Europe, where only three native species of *Acer* are widely available as potential hosts. Our now widened species limits for *H. wuestneii* entail the recognition of two different *Acer* species as its hosts: one in Central Europe, the other in the southern Balkans and Crete. Also, *Heterarthrus leucomela* has long been known to have two host species in Central Europe, so far without any evidence of genetic or morphological differences between the sawflies on the different host species. We conclude that the majority of West Palaearctic *Heterarthrus* species are oligophagous on several species within a single host plant genus, as has for example been recorded for *H. microcephalus* (Buhr 1941), *H. nemoratus* (Digweed et al. 2009, table 1), *H. ochropoda* (Arru 1967, Pschorn-Walcher and Altenhofer 2000), and *H. vagans* (Humble 2010).

The discovery of a previously undescribed but distinctive *Heterarthrus* species in Europe is a surprise. Because the only known place of occurrence of *vikbergi* is located in eastern Finland, close to the Russian border, it is tempting to speculate that it may also occur further east. The host plant species, *Populus balsamifera*, is native to North

America, with a transcontinental range from the northern limit of tree growth at about 68°N, southwards in the western mountains to about 42°N in Colorado (Zasada and Phipps 1990). In Europe, *P. balsamifera* is widely planted, mostly for amenity, and less so for timber. It is unlikely that *Heterarthrus vikbergi* originated in North America, because no natural occurrence of *Heterarthrus* is known from there. On the other hand, the appearance of *H. vikbergi* in large numbers on a species of plant growing outside its native range, suggests that the sawfly may have been introduced, or recently spread naturally from elsewhere. There seems little point in speculating further on this before we know more about the distribution and host associations of *H. vikbergi*.

Previous investigations suggest that DNA barcodes discriminate species of sawflies less effectively than in most other insect groups (Schmidt et al. 2017, Liston et al. 2017, Prous et al. 2016, 2017). This is especially true in Tenthredinidae, and particularly in its subfamily Nematinae, within which DNA barcode sharing between closely related species has been detected in many groups (Liston et al. 2017). Such problems may be attributable to increased levels of mitochondrial introgression in haplodiploid organisms (Patten et al. 2015, Sloan et al. 2017). Based on our data, species of *Heterarthrus* show a mean divergence between species of 4.47% and can mostly be reliably identified by their DNA barcodes (Fig. 1). Exceptions are the closely related species *H. cuneifrons*, *H. fiora* and *H. wuestneii*. Of these, *H. fiora* and *H. cuneifrons* show not even a single diagnostic nucleotide substitution in the DNA barcode region. On the contrary, it seems possible that *H. wuestneii* can be distinguished from these two species by its DNA barcode, although we have not been able to verify the identity of two analysed specimens (DEIGISHym19407 and DEIGISHym19408), which may belong to *H. cuneifrons* or *H. wuestneii*. A future effort to obtain sequences for some nuclear genes should be made to clarify the taxonomy of this species complex. The newly described *H. vikbergi* is well-characterized by its DNA barcode as showing a minimum of 6.07% divergence to its nearest neighbour *H. ochropoda*.

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