ACTA ENTOMOLOGICA MUSEI NATIONALIS PRAGAE
Published 31.xii.2017 Volume 57(2), pp. 677–711 ISSN 0374-1036
http://zoobank.org/urn:lsid:zoobank.org:pub:A7BE88CA-CC6F-4637-A2B2-17FBDD0B5EC0
https://doi.org/10.1515/aemnp-2017-0095

Anaphes flavipes: redescription, neotype designation, and comparison with *A. nipponicus* (Hymenoptera: Chalcidoidea: Mymaridae)

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Abstract. A neotype for *Anaphes flavipes* (Foerster, 1841) (Hymenoptera: Mymaridae), a biological control agent of *Oulema melanopus* (Linnaeus, 1758) (Coleoptera: Chrysomelidae), is designated. The extensive literature on *A. flavipes* is compiled and the morphological variability of selected morphological structures of numerous reared specimens from across its presently known geographic range (mainly eastern Nearctic and western Palearctic) is described. *Anaphes flavipes* is compared with what appears to be morphologically and biologically the most similar species, *A. nipponicus* Kuwayama, 1932, from Japan, which is briefly redescribed. *Anaphes auripes* Walker, 1846, syn. nov., is placed in synonymy under *A. flavipes*. The following new country and state records for *A. flavipes* are provided: Czech Republic, Ukraine, Canada (Nova Scotia), USA (Virginia).

Key words. Hymenoptera, Mymaridae, *Anaphes flavipes*, *Anaphes nipponicus*, biological control, neotype, morphological variability, new synonym, redescription, Holarctic Region

Introduction

Anaphes flavipes (Foerster, 1841) (Hymenoptera: Chalcidoidea: Mymaridae) belongs to the *fuscipennis* species group of *Anaphes sensu stricto*, as named and defined by Huber (1992). Viggiani (1994: 481), incidentally, named the *fuscipennis* group the *flavipes* group of species. The *fuscipennis* group contains 76 nominal species in the Holarctic Region, 67 of which were described, mostly by W. Soyka, from Europe (Huber 1992, 2004; Noyes 2016) and almost all of which are morphologically very similar and difficult to identify. *Anaphes*

flavipes is widespread in Europe where it parasitizes eggs of species of *Lema* Fabricius, 1798 and *Oulema* Des Gozis, 1886 (Coleoptera: Chrysomelidae), which are known as serious cereal pests in Europe. One of these pests, the cereal leaf beetle*, Oulema melanopus* (Linneaus, 1758), was accidentally introduced into North America in 1959 (Dysart et al. 1973). In the 1970s, the biology and ecology of *A. flavipes* was intensively studied (Anderson & Paschke 1968, 1969, 1970a,b; Moorehead & Maltby 1970a,b; Maltby et al. 1971, 1973). Anderson & Paschke (1968) showed that *A. flavipes* was able to develop in eggs of *Hypera zoilus* Scopoli, 1763 (Coleoptera: Curculionidae) and *Crioceris duodecimpunctata* (Linneaus, 1758) (Coleoptera: Chrysomelidae) under laboratory conditions but, nevetheless, *A. flavipes* was deliberately introduced into North America as a potential biological control agent of *O. melanopus* (Maltby et al. 1971). *Anaphes flavipes* is considered to be an important biological control agent of cereal leaf beetle (Haynes & Gage 1981, Horváth & Szabolcs 1992, Bai et al. 2004, Kimberling 2004, Jeloková & Gallo 2007) but Haynes & Gage (1985), cited by Mills (1990), stated that it had minimal impact.

Despite its use in biological control and the resulting extensive literature on *A. flavipes*, its identity is uncertain. Soyka (1949) had initially considered *A. flavipes* to be a species of *Gonatocerus* Nees, 1834, following Foerster (1841) but, evidently not realizing that Foerster (1847) himself had transferred it to *Anaphes* Haliday, 1833, Soyka did not include *A. flavipes* in his keys to *Anaphes* species. According to Soyka (1949: 310) Foerster's type material was mounted using minuten pins through the thorax, resulting in such "wrecks" that even the generic characters could not be seen.

Debauche (1948: 160) redescribed a species under the name *A.* (*Anaphes*) *flavipes* (Foerster) but did not see any of Foerster's type specimen(s). He made no mention of Foerster's material other than to cite his paper and state that Foerster's unique type came from Aix-la-Chapelle (French name for Aachen, Germany). He evidently did not search for the type of *A. flavipes* and if he did know where the type was deposited he apparently made no request to see it. He could not have known that the type was destroyed since Soyka (1949) only published that information a year later. Debauche provided measurements for only one of his own '*flavipes*' specimens although he had collected several females in June from reeds at the edge of ponds in the Parc abbey, Heverlee, Belgium, about 95 km from Aachen, Foerster's likely type locality, but he did not designate a neotype. Huber (1992) redescribed *A. flavipes* based on specimens from locations in Europe other than the type locality (no material had yet been collected from there). He did not designate a neotype, reasoning that specimens reared from *O. melanopus* are probably always *A. flavipes* so a neotype designation would be superfluous. But it is evident that several different species of *Anaphes* may indeed be reared from a given host, e.g., Huber et al. (1997), and to sort them out on the basis of morphology requires a type specimen for *A. flavipes* for comparison and objective definition of the species. At least two other nominal species of *Anaphes* have been reared from known hosts in the Criocerinae (Chrysomelidae): *A. nipponicus* Kuwayama, 1932 from *Oulema oryzae* (Kuwayama, 1932) [as *Lema oryzae* Kuwayama] in Japan (Kuwayama 1932) and an unidentified species from *Lilioceris lilii* Scopoli, 1763 and *L. merdigera* (Linnaeus, 1758) in Europe (Haye & Kenis 2004). Potentially, these spe-

cies could also occur on *O. melanopus*. Huber (1992) searched for Foerster's *A. flavipes* specimens in his pinned (i.e., mainly minuten pins) collection (NHMW) but failed to find any. A search by S. Triapitsyn (University of California at Riverside, USA) also yielded nothing under that name in Soyka's slide and pinned collections, although it is known that Soyka had remounted some of Foerster's specimens on slides including most of his types in NHMW. There is no doubt that Foerster's *A. flavipes* type(s) no longer exist(s). Because Debauche (1948) and Huber (1992) did not definitely solve the problem of the identity of *A. flavipes* it is important to define the name *A. flavipes* objectively by designating a neotype from among specimens reared by the second author from hosts collected at or near Aachen, Foerster's type locality for the species, in order to clarify its taxonomic status. This is even more important because *A. flavipes* belongs to a complex of *Anaphes* species whose species limits are poorly defined.

In this paper, we designate a neotype for *A. flavipes*, provide a diagnosis for it, compile the extensive literature on the species, describe morphological variability of selected morphological structures of numerous reared specimens from across its presently known geographic range (mainly eastern Nearctic and western Palearctic), and propose a new synonymy.

Materials and methods

Specimens of *A. flavipes* were reared from eggs of *Oulema melanopus* in Petri dishes under laboratory conditions (at Department of Zoology, Charles University, Prague, Czech Republic), stored in 96% ethanol at -20°C, and later slide-mounted following the procedure described by Noyes (1982) but without prior clearing in KOH and using propanol instead of ethanol. Slide-mounted specimens were photographed with a ProgRes C14^{plus} digital camera attached to a Nikon Eclipse E800 compound microscope, and the resulting layers were combined electronically using Auto-Montage® or Zerene Stacker™ and the images enhanced as needed with Adobe® Photoshop (no retouching of the neotype was done).

Terms used in the descriptions mostly follow Gibson (1997) except the ovipositor index, defined as ratio of ovipositor length to length of metatibia. Abbreviations used are: fl = funicle segment in female antenna or flagellar segment in male antenna, mps = multiporous plate sensillum or sensilla, OI = ovipositor index. All measurements are given in micrometers (μm). Bar graphs were calculated in STATISTICA, v. 12. One of us (JH) examined the lectotype of *A. auripes* Walker, 1846 for comparison with specimens of *A. flavipes*.

Collection acronyms are used as follows:

CNC	Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada;
DEBU	University of Guelph, Guelph, Ontario, Canada;
NHMW	Naturhistorisches Museum Wien, Vienna, Austria;
NMID	National Museum of Ireland, Dublin, Ireland;
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany;
USNM	National Museum of Natural History, Washington, D.C., USA;
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

Results

Anaphes flavipes (Foerster, 1841)

(Figs 1–13)

Gonatocerus flavipes Foerster, 1841: 45 (original description); Walker (1846): 53 (English translation of original description).

Anaphes flavipes: Foerster (1847): 212 (generic transfer, description); Loew (1847): 341 (taxonomy); Kirchner (1867): 202 (catalogue); Dalla Torre (1898): 423 (catalogue); Schmiedeknecht (1909): 499 (catalogue); Debauche (1948): 160 (redescription); Soyka (1949): 310 (moved [mistakenly] to *Gonatocerus*); Thanassoulopoulos (1967): 1 (potential host range); Anderson (1968): 6037 (distribution, ecology); Anderson & Paschke (1968): 1 (biology, ecology); Barton (1968): 3 (mass culture, field release); Anderson & Paschke (1969): 1316 (biology, superparasitism); Stehr (1969): 1 (biological control); Anderson & Paschke (1970a): 107 (biology); Anderson & Paschke (1970b): 821 (dispersal); Bakkendorf (1970): 154 (taxonomy of *A. flavipes sensu* Debauche); Barton & Stehr (1970): 128 (biology); Moorehead & Maltby (1970a): 675 (field release); Moorehead & Maltby (1970b): 1 (mass rearing); Bjegovic (1971): 176 (sex ratio, biological control, Yugoslavia [Serbia]); Burger et al. (1971): 1253 (laboratory preparation); Dysart (1971): 446 (European distribution, introduction into USA); Maltby et al. (1971): 693 (establishment in USA); Morris & Moorehead (1971): 41 (dispersal in USA: Michigan); Anonymous (1972): 1 (releases in USA); Bjegovic (1972): 207 (natural control); Burger & Holmes (1972): 1185 (mass production and dispersal); Carl (1972): 179 (host *Oulema melanopus*); Barr et al. (1973): 249 (pest control); Dysart et al. (1973): 157 (establishment in USA); Maltby et al. (1973): 298 (host, mass rearing); Miczulski (1973): 98 (natural control); Puttler et al. (1973): 1304 (diapause); Anonymous (1974): 2 (additional releases in USA); Dyadechko & Ruban (1974): 27 (host); Gutierrez et al. (1974): 627 (biology, host); Haynes et al. (1974): 167 (pest management); Hellén (1974): 24 (key), 25 (distribution in Finland and Leningradskaya oblast' of Russia); Olton & Legner (1974): 794 (biology); Stehr et al. (1974): 453 (mention); Aeschlimann (1975): 407 (mention); Tummala et al. (1975): 175 (natural control); Anonymous (1976a): 414 (host, USA: Maryland, Pennsylvania, West Virginia records); Anonymous (1976b): 369 (host, USA: New Jersey, West Virginia records); Anonymous (1976c): 420 (host, USA: Ohio record); Greathead (1976): 128 (biological control); Hagen et al. (1976): 398, 746 (biological control); Meyer (1976): 232 (USA: Indiana record); Aeschlimann (1977): 112 (larvae, biology); Bouček (1977): 122 (Yugoslavia [Serbia, Macedonia?] records); Lutze (1977): 172 (biological control, percent parasitism); Pavlov (1977): 151 (percent parasitism, sex ratio, development time); Shepard & Gale (1977): 316 (biology, superparasitism); Clausen (1978): 253 (biological control); Ryakhovskiy & Krakhmal' (1978): 30–32 (records from Rostovskaya oblast' and Krasnodarskiy kray, Russia, from *O. melanopus* [as *Lema melanopus*]); Trjapitzin (1978): 531 (key); Burks (1979): 1029 (catalogue); Peschken & Johnson (1979): 1061 (host, parasitation); Akers et al. (1980): 34 (biological control); Burger (1980): 39 (biological control); Botterweg (1981): 170 (biology); Haynes & Gage (1981): 269 (biological control); Hinton (1981): 238 (percent parasitism); Pavlov (1981): 116, 122 (hosts, Bulgaria record); Battenfield et al. (1982): 291, 292, 295, 296, 299 (*Oulema melanopus* bibliography); Fedde et al. (1982): 382 (list); Webster et al. (1982): 839 (occurrence, parasitation); Collins & Grafius (1983): 2 (hosts); Lampert et al. (1983): 972, 973, 978 (pest control, parasitism rate); McPherson (1983): 127 (parasitism rate, biological control); Staines (1984): 435 (parasitism rate); Lampert & Haynes (1985): 74 (parasitism rate); Collins & Grafius (1986): 31 (courtship, mating behavior); Huber (1986): 197 (host list); Davidson & Lyon (1987): 178 (biological control); Donev (1987): 69 (percent of parasitism, sex ratio); Hua (1987): 41 (percent of parasitism, laboratory rearing, hosts); Trjapitzin (1987): 964 (key); Viggiani & Jesu (1988): 1021 (biological control); Ellis et al. (1989): 43 (absence of parasitism); Głogowski (1989): 240 (in moist meadows, Poland); Haeselbarth (1989): 494, 495 (host, mention); Ruberson (1989): 190 (biology); Burgess (1990): 6 (biological control); Miura (1990): 589 (biology); Bailey et al. (1991): 457 (biological control); Picard et al. (1991): 173, 174 (citation with comparison); Szabolcs & Horváth (1991): 166–169, 172 (biological control, occurrence); Horváth & Szabolcs (1992): 585, 586, 589 (biological control, Hungary); Huber (1992): 36, 47, 74 (key, redescription, biological control, list); Furukawa et al. (1993): 92 (host); Cox (1994): 430 (biological control); Messing et al. (1994): 976 (host, natural control); Schärer (1994): 21 (parasitism rate, phenology); Morrill (1995): 93 (biological control); Pagliano & Navone (1995): 35 (Italy, check list); Mayhew (1997): 238 (clutch size); Kidd (1998): no page (biological

control); Kidd & Caldwell (1998): no page (biological control); Milevoj (1998): 216 (host, monitoring); Bai & Worth (2000): 1–4 (biological control); Fournier & Boivin (2000): 59 (biology); Bai et al. (2001): 1–3 (biological control, distribution); Meindl et al. (2001): 79–81, 83–85 (parasitism rate); Vail et al. (2001): 44 (biological control); Glogoza (2002): 2 (natural control); Hitchcox et al. (2002): 8, 9 (biological control); Yokoyama & Miller (2002): 513 (biological control); Bai et al. (2003): 1 (biological control); Kidd (2003): 9, 10 (biological control); Olson et al. (2003): 3 (biological control); Santolamazza-Carbone & Rivera (2003): 370 (biology); Blodgett et al. (2004): 4 (biological control); Casagrande & Kenis (2004): 123, 133 (biological control); Haye & Kenis (2004): 404 (biological control); Kimberling (2004): 313 (biological control); Popov et al. (2005): 49 (natural control, monitoring); Trudgill (2005): 7 (biology); Bai et al. (2006): 1 (biological control); Evans et al. (2006): 1968 (biological control, distribution); Godfrey et al. (2006): 4 (biology); Hoffman & Rao (2006): 43 (expansion, biological control); Jandreau (2006): 1 (biological control); Santolamazza-Carbone (2006): 373 (biology); Traoré et al. (2006): 1122 (biology); Brown & Park (2007): 2 (biological control); Gallo (2007): 446, 447 (parasitism, host *Oulema lichenis*); Lesage et al. (2007): 288 (biological control); Pike et al. (2007): 1–4 (survival of insecticides); Wabeke (2007a): 9 (monitoring); Wabeke (2007b): 40 (biological control); Jandreau (2008): 1, 4 (biological control); Jeloková & Gallo (2008): 109, 112 (biological control, monitoring); Johnson et al. (2008): 2 (biological control); Karren (2008): 2 (biological control); Peairs (2008): 4234 (biological control); Pricop (2008): 124 (distribution); Mills (2009): 394 (biological control); Hoffman & Rao (2010): 57 (biological control); Laznik et al. (2010): 142 (biological control); Dosdall et al. (2011): 1145 (biological control); Philips et al. (2011): 3 (biological control); Baquero (2012): 7, 9, 138 (biological control); Pintureau (2012): 34 (European list); Roberts & Rao (2012): 6 (biological control); Bucurean & Marnea (2013): 30, 31 (natural control, parasitism rate); Kamran et al. (2013): 174 (host); Kher et al. (2013): 234, 487, 497 (biological control); Makarova & Polilov (2013): 714 (brain structure); Kher (2014): 23, 26, 27 (biology, biological control); Puttler et al. (2014): 34 (mention); Tewksbury (2014): 4, 5 (introduction, biology); Makarova et al. (2015): 21, 23 (compound eye, morphology); Nordijk et al. (2016): 5 (hosts); Polilov (2016): 407 (internal anatomy); Roberts (2016): 878 (release in Washington State, USA).

Anaphes (*Anaphes*) *flavipes*: Yoshimoto (1990): 52 (list); Viggiani (1994): 474, 480 (male genitalia, key).

Anaphes sp.: Stehr (1969): 1 (biological control).

Patasson valkenburgica (misidentification): Bakkendorf (1964): 3 [see Bakkendorf (1970): 153 for correction].

Anaphes lemae Bakkendorf, 1970: 153 (original description); Miczulski (1973): 98 (natural control); Bouček (1977): 122 (Yugoslavia [Serbia] record); Trjapitzin (1978): 531 (key, record from Voronezhskaya oblast', Russia); Collins & Grafius (1983): 2 (hosts); Trjapitzin (1987): 964 (key); Viggiani & Jesu (1988): 1021 (synonymy under *A. flavipes*); Huber (1992): 48 (synonymy under *A. flavipes*).

Anaphes auripes Walker, 1846: 52 (original description); Dalla Torre (1898): 423 (catalogue); Schmiedeknecht (1909): 499 (catalogue); Kloet & Hincks (1945): 304 (British checklist); Bouček & Graham (1978): 110 (British checklist); Graham (1982): 192, 209 (redescription, lectotype designation); Huber (1992): 72 (list); Thuróczy & O'Connor (2015): 56 (Ireland records, lectotype image); Dale-Skey et al. (2016): 232 (British checklist). **New junior subjective synonym.**

Mymar auripes: Soyka (1949): 310 (list).

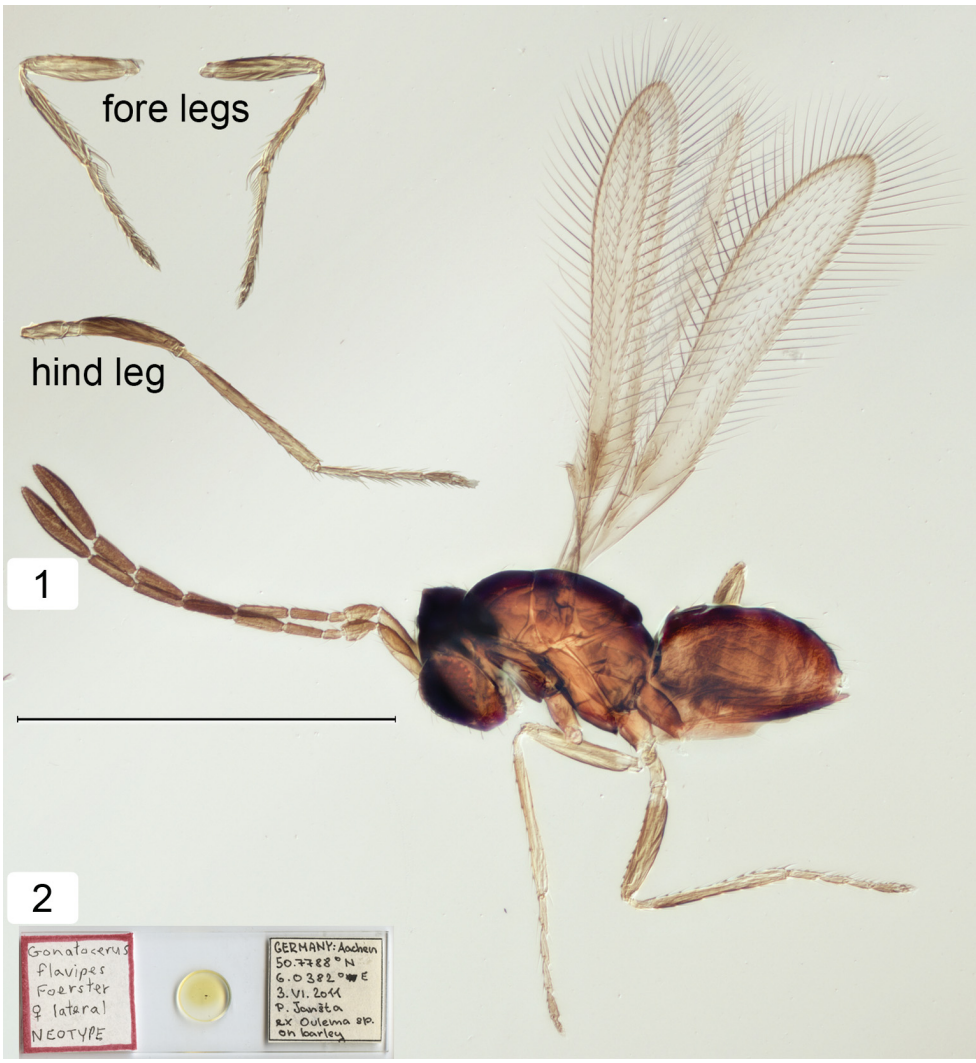
Type locality. *Anaphes flavipes*: 'Aachen' [environs of Aachen, North Rhine-Westphalia, Germany]; *Anaphes auripes*: 'England' [almost certainly Southgate vicinity]; *Anaphes lemae*: 'Poland, Lublin (city area)' [= Lublin Voivodeship].

Type material examined. *Gonatocerus flavipes*: Neotype: ♀ (here designated to avoid ambiguity about the identity of this species, whose type material is lost) (Fig. 1); on slide labelled as shown (Fig. 2): 'Gonatocerus | flavipes | Foerster | ♀ lateral | NEOTYPE || Germany: Aachen | 50.7788°N | 6.0382°E | 3.vi.2011 | P. Janšta | ex Oulema sp. | on barley' (NHMW).

Anaphes auripes: Lectotype: ♀ (designated by Graham (1982): 209, on card and labelled as shown in Fig. 11): 'Anaphes | auripes | Walker | LECTOTYPE: ♀ | M.de V. GRAHAM | det. 1972 || 9.' (NMID).

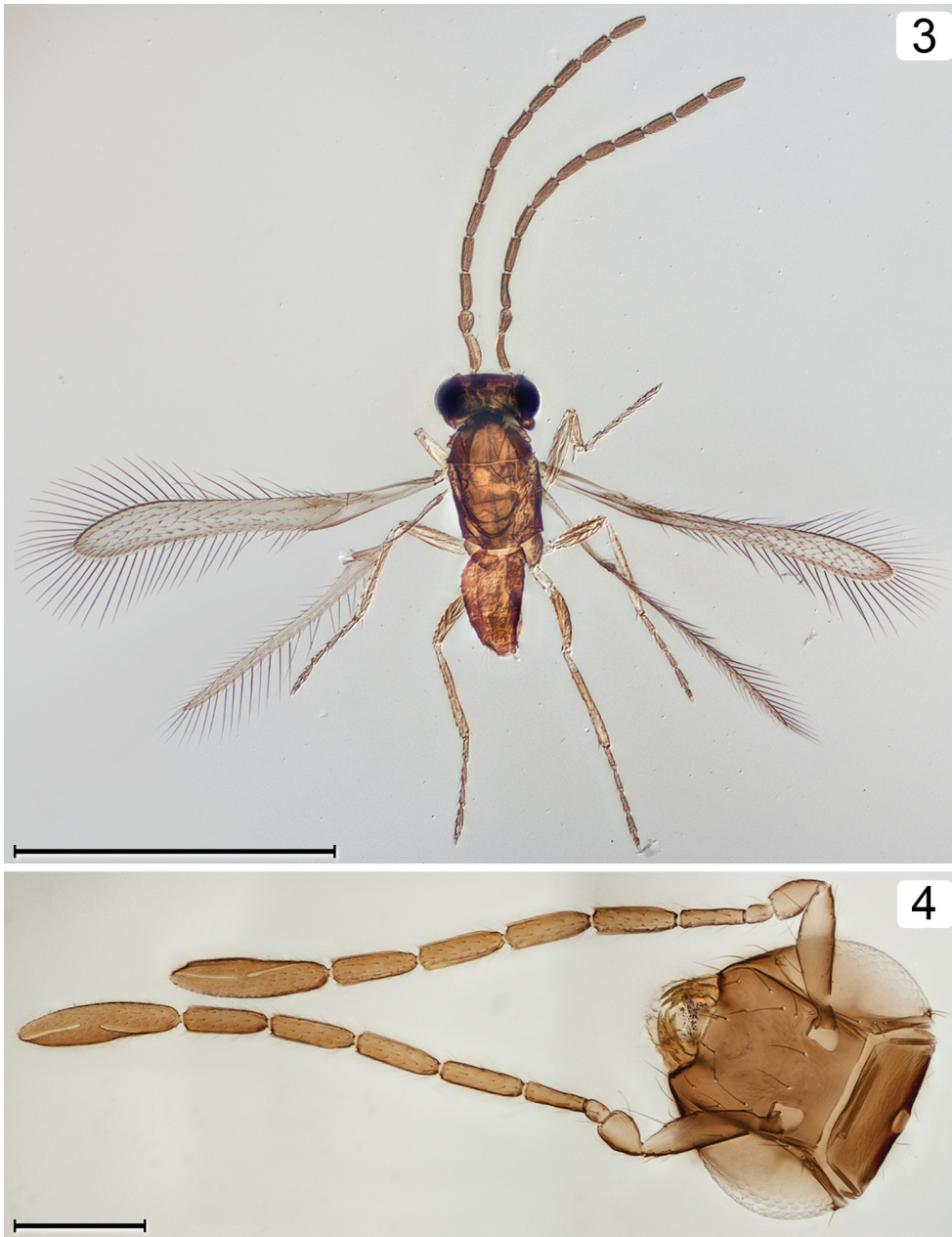
Anaphes lemae: Holotype: ♀ (examined by Huber 1992: 48) (ZMUC).

Additional material examined (all in CNC unless otherwise indicated). **AUSTRIA: Wien:** Vienna, Obere Lobau Nature, Reserve, 23.v.1996, B. Bartl, ex *Oulema melanopus*, in organically cultivated winter wheat field (5 ♀♀); No locality, vi.1968, G. E. Moorehead (4 ♀♀ 2 ♂♂, USNM). **CANADA: Ontario:** Delhi, 25.v.1988, C. Ellis

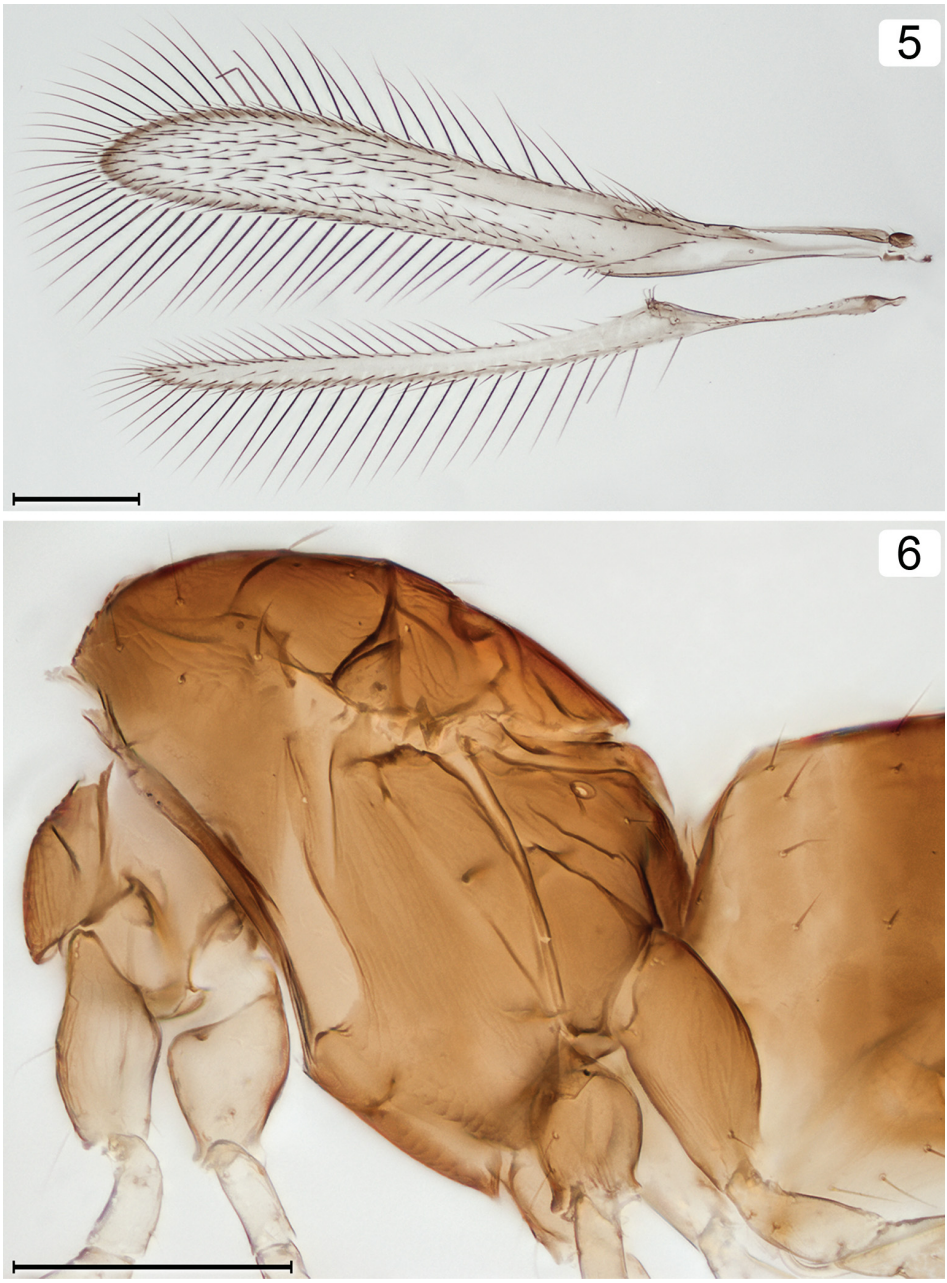


Figs 1–2. *Anaphes flavipes* (Foerster, 1841). 1 – neotype female (uncleared), dorsolateral habitus (fore legs and left hind leg above antennae); 2 – neotype slide. Scale bar: 500 μm.

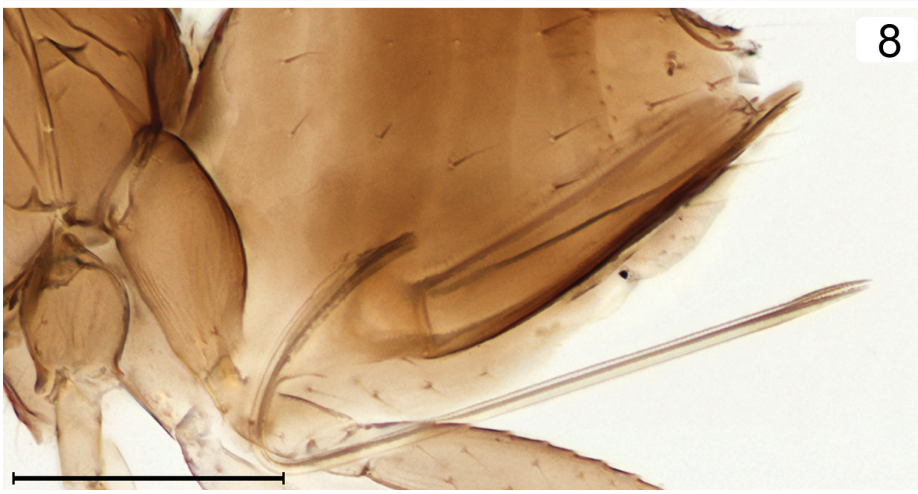
(1 ♀, DEBU). **Nova Scotia:** lot#95 FRN881-F93 from USDA-Aphis-PPQ, Niles, MI, 18.vi.1998, L. Crozier (5 ♀♀). **CZECH REPUBLIC: Bohemia:** Mečeříž, 50°17′24.07″N, 14°44′09.37″E, 28.v.2009, I. Králová & A. Samková, ex *Oulema* sp., wheat field (1 ♀); Praha, 50°8′18.78″N, 14°22′11.00″E, 26.iv.2010 (2 ♀♀), 11.vi.2010 (1 ♀), A. Samková, ex *Oulema*, barley field; Roudné u Českých Budějovic, 48°56′6″N, 14°29′15″E, 24.v.2010, A. Samková, ex *Oulema* sp., barley field (3 ♀♀); Velký Újezd, 49°34′42.92″N, 17°28′59.19″E, 26.v.2011, A. Samková, ex *Oulema* sp., wheat field (1♀). **FRANCE:** Nanterre, 7.vii.1964, G.W. Angalet, 28.v.1965, R. I. Sailer



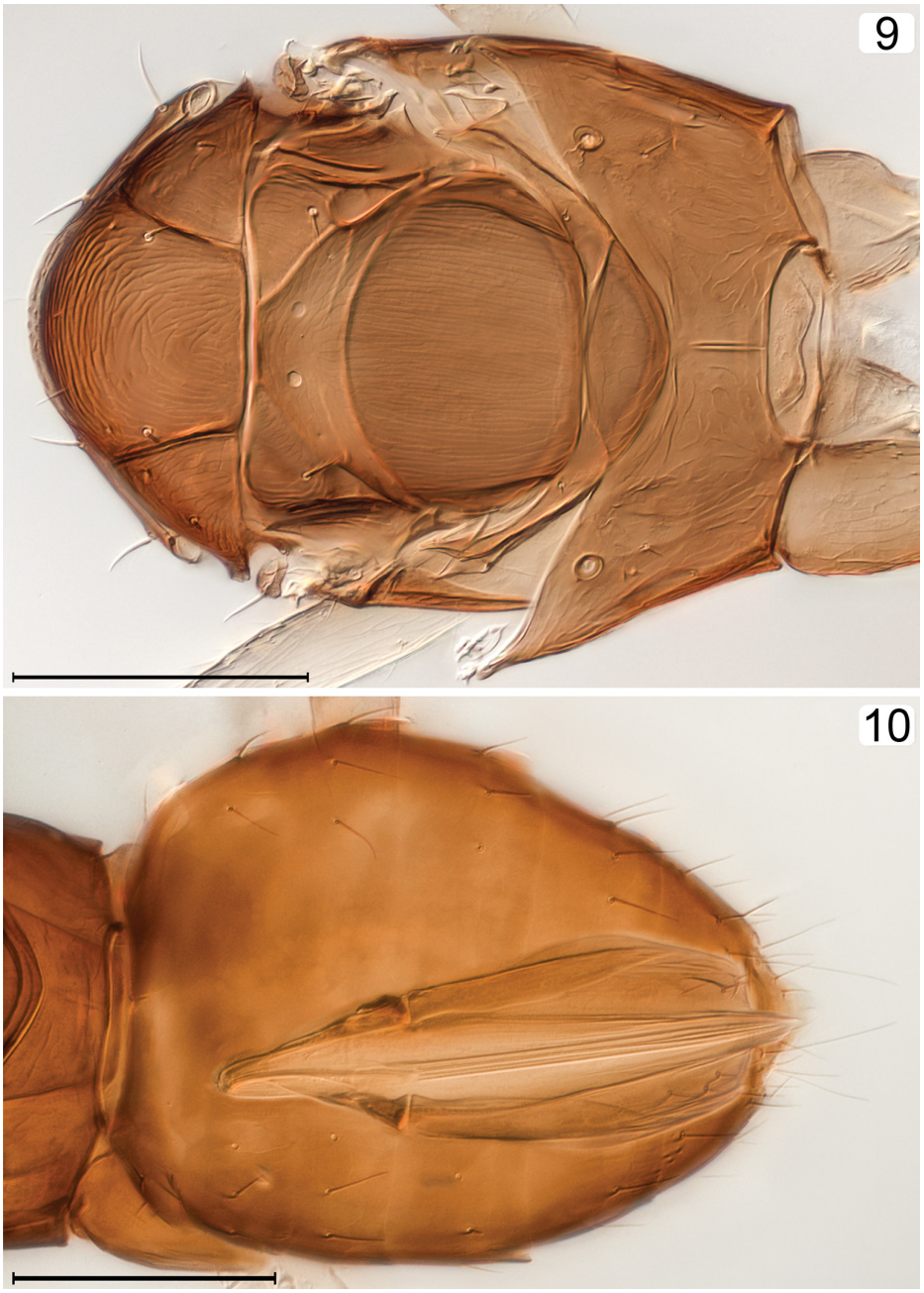
Figs 3–4. *Anaphes flavipes* (Foerster, 1841). 3 – male habitus, dorsal view (uncleared, with same collection data as neotype); 4 – female head (anterior) and antennae. Scale bars: 3 – 500 µm; 4 – 100 µm.



Figs 5–6. *Anaphes flavipes* (Foerster, 1841), female. 5 – fore wings; 6 – mesosoma, lateral view. Scale bars: 100 µm.



Figs 7–8. *Anaphes flavipes* (Foerster, 1841), female. 7 – body (minus head), lateral view; 8 – metasoma, lateral view. Scale bars: 100 µm.



Figs 9–10. *Anaphes flavipes* (Foerster, 1841), female. 9 – mesosoma, dorsal view; 10 – metasoma, dorsal view showing genitalia through gaster. Scale bars: 100 μm.

(2 ♀♀, USNM); Tours, 27.vi.1968 (10 ♀♀ 5 ♂♂, USNM), 16.vi.1970 (4 ♀♀, USNM), L. Dureseau; Sèvres, 2–4. vi.1972, R. Dysart, E. Rivet, ex *Oulema melanopus* or *O. gallaeciana* (Heyden, 1870) (2 ♀♀). **GERMANY: North Rhine-Westphalia:** Aachen, 50.77876°N, 06.03816°E, 3.vi.2011, P. Janšta, A. Samková, ex *Oulema* spp. (35 ♀♀ 3 ♂♂); Aachen, 50.77876°N, 06.03816°E, 25.vi.2012, P. Janšta, A. Samková, ex *Oulema* spp. (7 ♂♂). **ITALY: Lazio:** Rome, 17.v.1965, J. J. Drea (1 ♀, USNM); no locality, no month, 1965–1967, European parasite lab. staff, ex *Oulema* sp. (6 ♀♀). **POLAND:** no locality, 17.xii.1969, G. E. Moorehead (23 ♀♀ 11 ♂♂, USNM). **ROMANIA: Mureș Co.:** Reghin, 30.v.1968, R. Dysart, L. Coles, ex *Oulema melanopus* (7 ♀♀); no locality, vi.1968, G. E. Moorehead (2 ♀♀ 2 ♂♂, USNM). **UKRAINE and/or RUSSIA:** Kiev and/or Krasnodar, 1–3. vii.1970, ex *Oulema gallaeciana* (5 ♀♀). **USA: Michigan:** Allegan Co., 29.iv.1968, T. L. Burger (3 ♀♀, USNM); Berrien Co.: Bertrand Township, 3.vii.1975, P. R. DeWitt (2 ♀♀ 2 ♂♂, USNM); Berrien Co., 1971 (2 ♀♀); Niles, 6.vii.1967, 2.x.1967, 10.vii.1969, 12.vi.1970, H. Maltby, T. L. Burger, F. Wilkinson, G. E. Moorehead (41 ♀♀ 14 ♂♂, USNM), 1975 (5 ♀♀, USNM), 1977 (11 ♀♀ 7 ♂♂); Branch Co., 1975 (23 ♀♀, USNM); St. Clair Co., 1975 (15 ♀♀, USNM). **Maryland:** Baltimore Co., 1975 (18 ♀♀, USNM); Washington Co., 25.vii.1975, P. R. DeWitt (2 ♀♀ 2 ♂♂, USNM), 1975 (14 ♀♀, USNM). **New York:** Ontario Co., 1973, ex *Oulema melanopus* (1 ♀); Ontario Co., 1975 (13 ♀♀, USNM). **North Carolina:** Granville Co., 17.v.1991, D. I. Puttler, ex *Oulema melanopus* (3 ♀♀); Granville Co., 17.v.1991, B. I. Puttler (4 ♀♀ 1 ♂); Rowan Co., 16.v.1991 (15 ♀♀ 3 ♂♂). **Pennsylvania:** Armstrong Co., 25.vii.1975, P. R. DeWitt (3 ♀♀ 1 ♂, USNM), 1975 (17 ♀♀, USNM). **Virginia:** Hanover Co., 14.v.1991, J. Tate, ex *Oulema melanopus* (3 ♀♀). **West Virginia:** Mason Co., 1975 (19 ♀♀, USNM). **SERBIA:** Zemun, no month, 1966–1968, P. Bjegovic, ex *Oulema* sp. (7 ♀♀); no locality, 18.viii.1967, T. L. Burger (12 ♀♀ 3 ♂♂, USNM); no locality or date, P. Bjegovic (5 ♀♀, USNM).

Diagnosis. Females of *Anaphes flavipes* are distinguished from those of other *Anaphes* species by the following combination of features: clava 1-segmented, at least 3.9× as long as wide; fl_2–fl_6 each with 2 mps; fl_2 at least 2.5× as long as wide; fore wing at least 5.5× as long as wide; metatarsomere 1 equal to or slightly shorter than 2; OI about 1.0.

Description. Neotype female (Fig. 1). Uncleared, mounted laterally with three legs detached, on slide (Fig. 2). Body length 610. Colour. Body and antenna fairly uniform brown; legs except coxae light brown to yellow except metafemur and metatibia darker (Fig. 1). Antenna. Length/width (ratio) of segments: scape 110/29 (3.79), pedicel 48/26 (1.85), fl_1 28/13 (2.15), fl_2 52/15 (3.47), fl_3 69/22 (3.14), fl_4 71/23 (3.09), fl_5 72/20 (3.60), fl_6 67/23 (2.91), clava 126/27 (4.67); fl_3–fl_6 each with 2 mps. Total flagellum length 485. Wings. Fore wing length/width (ratio) 707/110 (6.43); longest marginal setae about 140, marginal space length 100, with single line of setae separating marginal space from hind margin (Fig. 1). Hind wing length/width (ratio) 702/33 (21.27), with 10 microtrichia in 1 median row in apical half of wing beyond venation; longest marginal setae about 120. Legs. Metatibia length 246; metatasomere 1 0.96× length of metatarsomere 2. Metasoma. Ovipositor length 250, extending under mesosoma to about level of mesocoxa; OI 1.02.

Variation in non-type specimens. ***Female*** (Figs 4–10). Body length (n = 10) excluding ovipositor 409–657. Head width (n = 89, slide-mounted females, 5 from Austria, 5 from Canada, 8 from Czech Republic, 2 from France, 35 from Germany, 6 from Italy, 7 from Romania, 7 from Serbia, 5 from Ukraine and/or Russia and 9 from USA) 201–281. Length/width of segments: fl_1 20–34/12–18, fl_2 24–72/13–35, fl_3 48–87/16–26, fl_4 52–89/16–28, fl_5 52–87/15–30, fl_6 52–85/17–28, clava 107–151/26–42. Total flagellum length 405–605. Mesosoma. Fore wing length/width 529–821/69–145. Metatibia length 175–310. Metasoma. Ovipositor length 200–309; OI 0.9–1.4.

Male (Fig. 3). Body length 385–665 (n = 50, critical point dried and point- or card-mounted specimens, 30 from North America and 20 from Europe). Similar to female except as

follows. Length/width of segments (n = 10, slide-mounted specimens from Germany): head width 185–228, pedicel 37–48/23–33, fl_{1+2} 58–88/17–22, fl_3 58–82/17–22, fl_4 62–80/17–22, fl_5 62–82/17–22, fl_6 60–82/17–22, fl_7 58–83/17–22, fl_8 57–82/17–23, fl_9 57–80/17–23, fl_{10} 55–82/18–23, fl_{11} 63–82/17–22. Total flagellum length 590–815. Fore wing length/width 640–840/85–118, hind wing length/width 590–770/25–33. Metatibia length 200–207. Genitalia shown in Fig. 10. Viggiani (1994) measured 7 features of the male genitalia from 20 specimens in each of 4 allopatric populations (Italy, former Yugoslavia, Poland and Romania) of *A. flavipes* and found no significant differences among them.

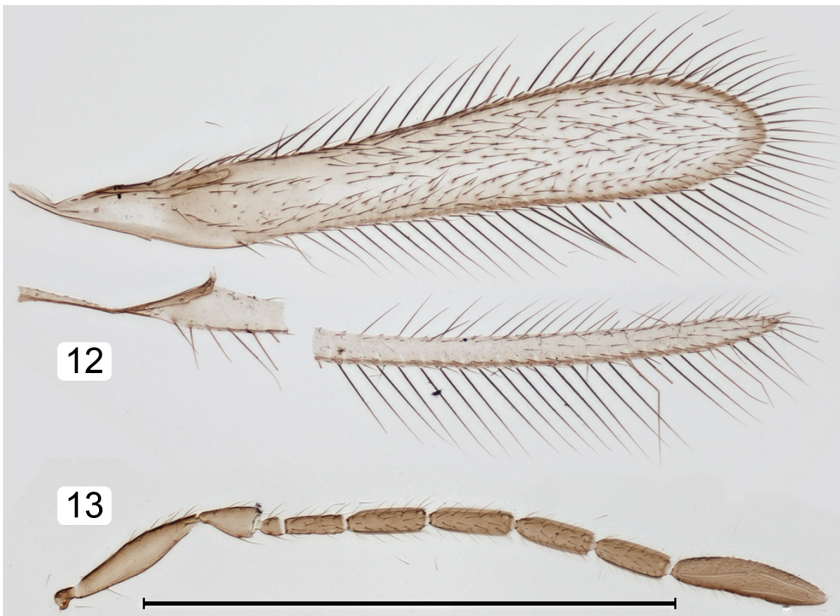
Ratios of all measurements as well as minimum and maximum values for each measured structure of 89 females of *A. flavipes* from different localities across the distribution and 10 males of *A. flavipes* from Germany are tabulated (Appendices 1 and 2). Absolute measurements are also plotted as bar graphs (Appendix 3); all these measurements are accessible on request from the authors.

Hosts. *Lema trilinea* White, 1981 (Burger & Holmes 1972, as *L. trilineata* Olivier, 1808), *Oulema gallaeciana* Heyden, 1870 [= *Crioceris obscura* Stephens, 1831 and Bakkendorf 1970, as *L. lichenis* Voet, 1806], *Oulema collaris* (Say, 1824), *O. melanopus* (Linneaus, 1758), the cereal leaf beetle (Coleoptera: Chrysomelidae). Under laboratory conditions *Crioceris duodecimpunctata* (Linnaeus, 1758) (Chrysomelidae) and *Hypera zoilus* Scopoli, 1763 (Curculionidae) were also parasitized (Anderson & Paschke 1968).

Distribution. Palearctic Region: Austria (Huber 1992, as *A. flavipes*), Bulgaria (Pavlov 1981, as *A. flavipes*), Czech Republic (new record), Finland (Hellén 1974, as *A. flavipes*), France (Huber 1992, as *A. flavipes*), Germany (Foerster 1841), Hungary (Horváth & Szabolcs 1992, as *A. flavipes*), Ireland (Thuróczy & O'Connor 2015, as *A. auripes*), Italy (Huber 1992, as *A. flavipes*), Macedonia? (Bouček 1977, as *A. flavipes*), Poland (Huber 1992, as *A. flavipes*), Romania (Huber 1992, as *A. flavipes*), Russia (Hellén 1974, as *A. flavipes*; Ryakhovskiy & Krakhmal' 1978, as *A. flavipes*; Trjapitzin 1978, as *A. lemae*), Serbia (Bouček 1977, as *A. flavipes*), United Kingdom (Dale-Skey et al. 2016, as *A. auripes*), Ukraine (new record), Yugoslavia (Huber 1992, as *A. flavipes*). **Nearctic Region**: Canada: Ontario (Huber 1992, as *A. flavipes*), Nova Scotia (new record), USA: Indiana (Meyer 1976, as *A. flavipes*), Maryland (Huber 1992, as *A. flavipes*), Michigan (Huber 1992, as *A. flavipes*), New Jersey (Anonymous 1976b, as *A. flavipes*), New York (Huber 1992, as *A. flavipes*), North Carolina (Huber 1992, as *A. flavipes*), Ohio (Anonymous 1976c, as *A. flavipes*), Pennsylvania (Huber 1992, as *A. flavipes*), Virginia (new record), Washington (Roberts 2016, as *A. flavipes*), West Virginia (Huber 1992, as *A. flavipes*).

Comments. A neotype is designated with the express purpose of clarifying the taxonomic status of *G. flavipes* Foerster. The neotype is distinguished from similar species in the speciose (about 240 nominal species) and difficult genus *Anaphes* by the following combination of features: fl_1 and fl_2 without mps, remaining funicle segments with 2 mps and, except for fl_1, at least 2.5× as long as wide; clava 1-segmented; fore wing 6.4× as long as wide and slightly pointed; and ovipositor length 1.0× metatibia length. Its measurements are given above and it is illustrated in Fig. 1. Foerster's collection was partially destroyed (Soyka 1949: 310) and JH confirmed this when he was unable to find Foester's material of *G. flavipes* during a visit to NHMW. The specimens selected as neotype is from or very near the Foerster's type locality

Fig. 11. *Anaphes auripe*s Walker, 1846, lectotype female and lectotype labels. Scale bar: 500 µm.



Figs 12–13. *Anaphes auripes* Walker, 1846, lectotype female. 12 – wings; 13 – antenna. Scale bars: 500 µm.

(Aachen or environs) and fits his brief description and redescription fairly well. It will be deposited in NHMW, where most remaining Foerster specimens are deposited.

The measurements of the lectotype of *A. auripes* fall well within the range of variation for *A. flavipes*, e.g., length/width ratio of funicle segments: fl_1 1.5, fl_2 3.2, fl_3 3.4, fl_4 3.6, fl_5 3.1, fl_6 2.8, clava 4.4; wing length/width ratio 6.4; and ovipositor length/metatibia length ratio1.0, so our synonymy is justified.

Anaphes nipponicus Kuwayama, 1932

(Figs 14–26)

Anaphes nipponicus Kuwayama, 1932: 93 (original description); Clausen (1940): 100 (egg production); Thompson (1958): 568 (Taiwan [as Formosa], Japan); Yasumatsu & Watanabe (1965): 65 (host); Hirashima (1989): 644 (check list for Japan); Storozheva (1989): 14–16 (host, biology, Primorskiy kray, Russia); Storozheva (1990a): 113 (biology); Storozheva (1990b): 29 (percent of parasitism, biology); Furukawa et al. (1993): 92 (host); Roberts (2016): 878 (collection in China).

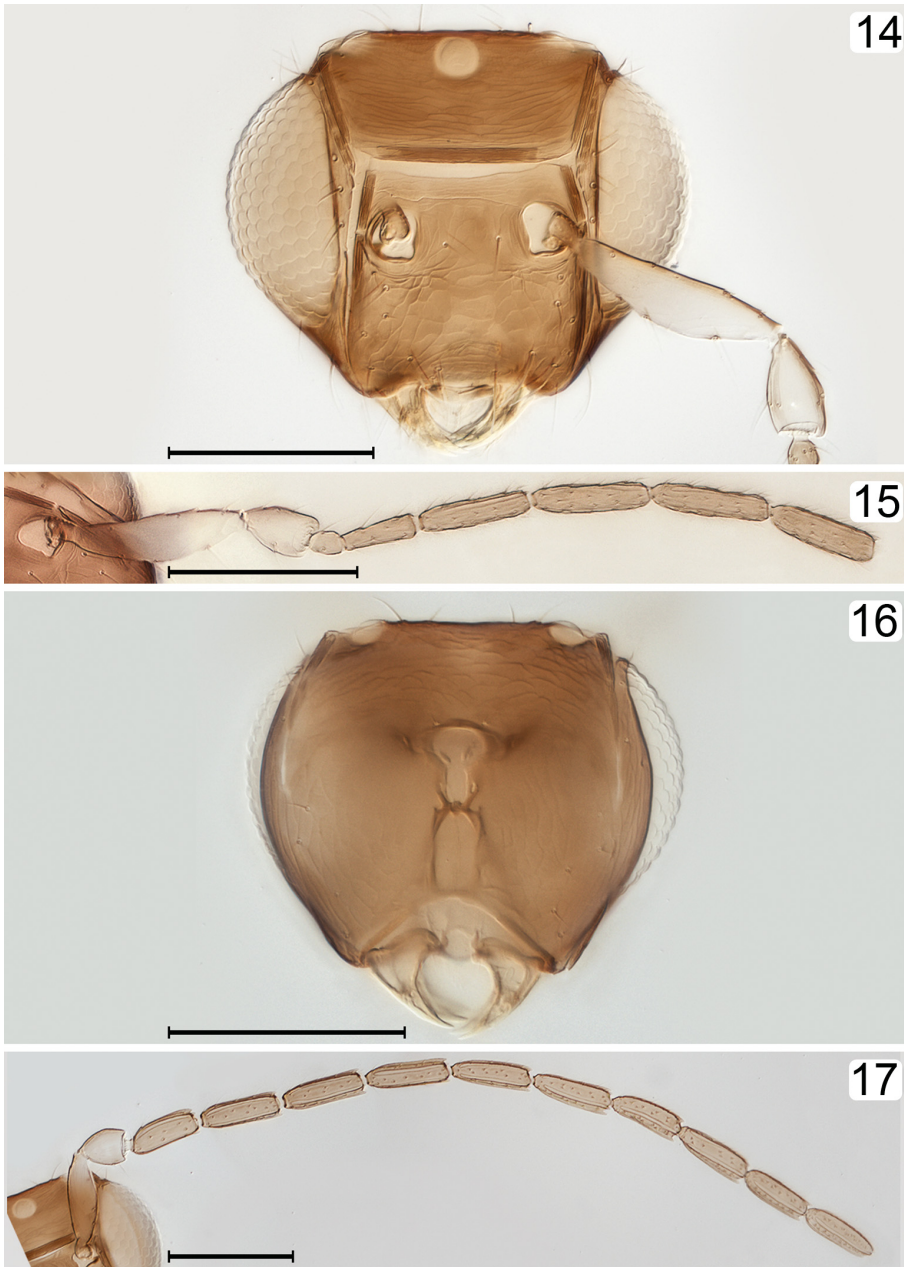
Type locality. *Anaphes nipponicus*: 'Japan, Hokkaido, Ôno, Kameda District, 41°56′N 149°41′E and Kagura, Kamikawa District, 43°46′N 142°44′E'.

Type material. Kuwayama (1932: 95) stated that the species was described from many co-type specimens mounted in balsam, "euparal", dry, and in alcohol. Kamijo K. (personal communication, October, 2014) stated that the Kuwayama collection was moved from the Hokkaido Agricultural Research Centre [originally Hokkaido Agriculture Experiment Station] to the National Institute for Agro-Environmental Sciences (NAIES), Tsukuba. There, they cannot be located and therefore could not be borrowed for study.

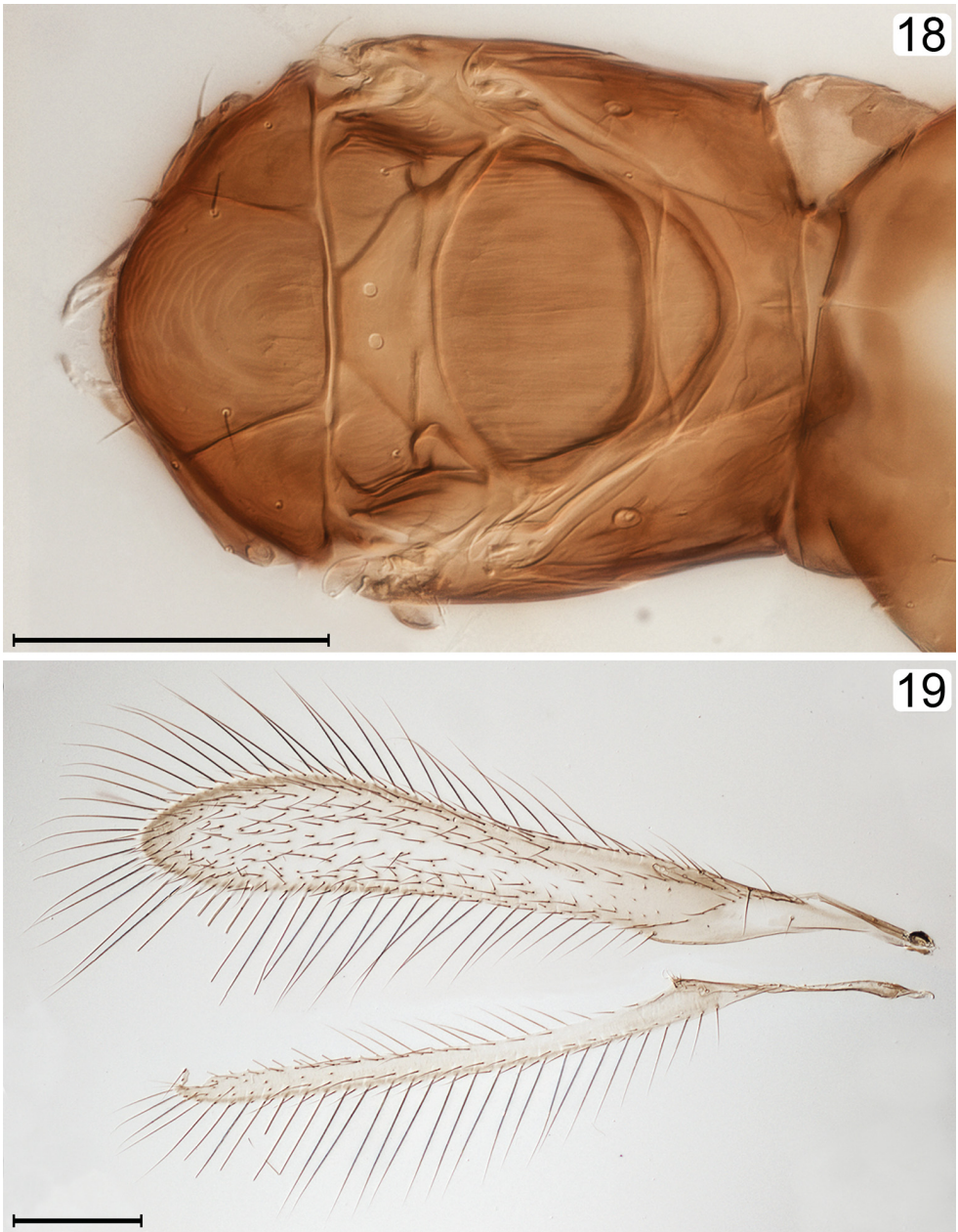
Material examined. JAPAN: Hokkaidó: Naganuma, Sorachi, 9.vii.1987, S. Takakawa (3 ♀♀ 1 ♂, CNC).

Comments. The four non-type, card-mounted specimens listed above were reared from *Lema oryzae*; they were unglued from their cards, cleared and slide-mounted in Canada balsam, and are redescribed (below). The collection locality is about 30 km from Kagura [present day Higashikagura, Kamikawa subprefecture], one of the two type localities for *A. nipponicus*. The redescription, based on these specimens, is given for comparison with *A. flavipes*. Because the measurements of the metatarsal segments and fore wing are from a male of *A. nipponicus*, the differences are not strictly comparable with the same measurements taken from females of *A. flavipes*. Nineteen specimens (17 ♀♀ 2 ♂♂ – SDEI), each on its own slide (Fig. 26, photographed and identified as *A. auripes* by C. Thuróczy), and at least five of which were identified as *A. nipponicus* by Kuwayama, are uncleared and poorly mounted in Canada balsam. Because the specimens are not from the type localities but instead from Kotoni, Sapporo, and were collected on 10.vii.1931, instead of in 1928 or 1929 (Kuwayama 1932: Tables 26 and 27), they cannot be considered as syntypes.

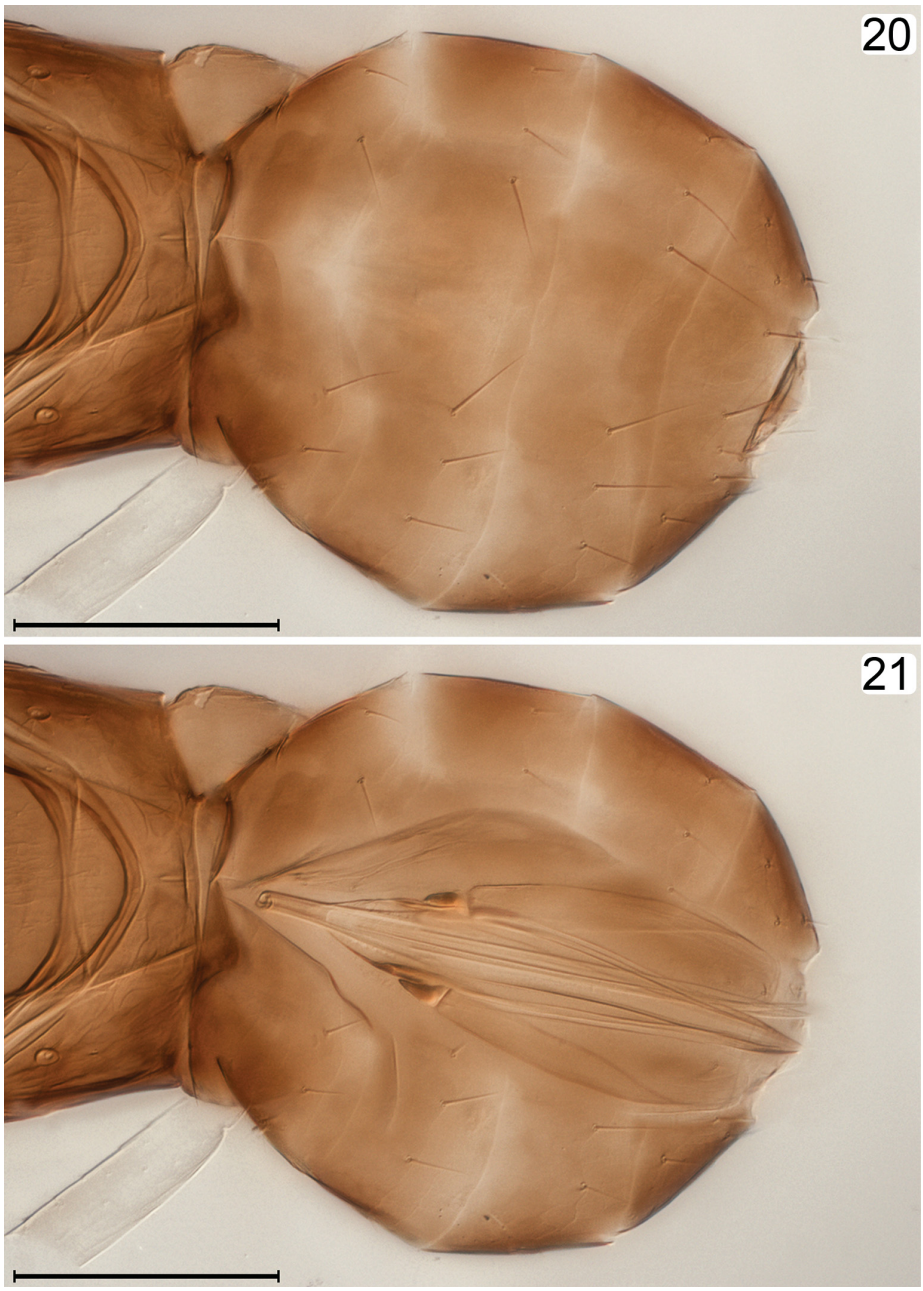
Diagnosis. *Anaphes nipponicus* differs from *A. flavipes* as follows: marginal space shorter (longer in *A. flavipes*); fore wing wider with slightly more rounded apex (slightly narrower with slightly more pointed apex in *A. flavipes*), frenum with campaniform sensilla slightly closer together (slightly farther apart in *A. flavipes*), metatarsomere 1 clearly shorter than (0.75 as long as) metatarsomere 2 (at most or only slightly shorter in *A. flavipes*). There may also be differences in relative proportions of wings, antennal segments and the ovipositor/metatarsus ratio but more females of *A. nipponicus* must be reared and measured for comparison with *A. flavipes*.



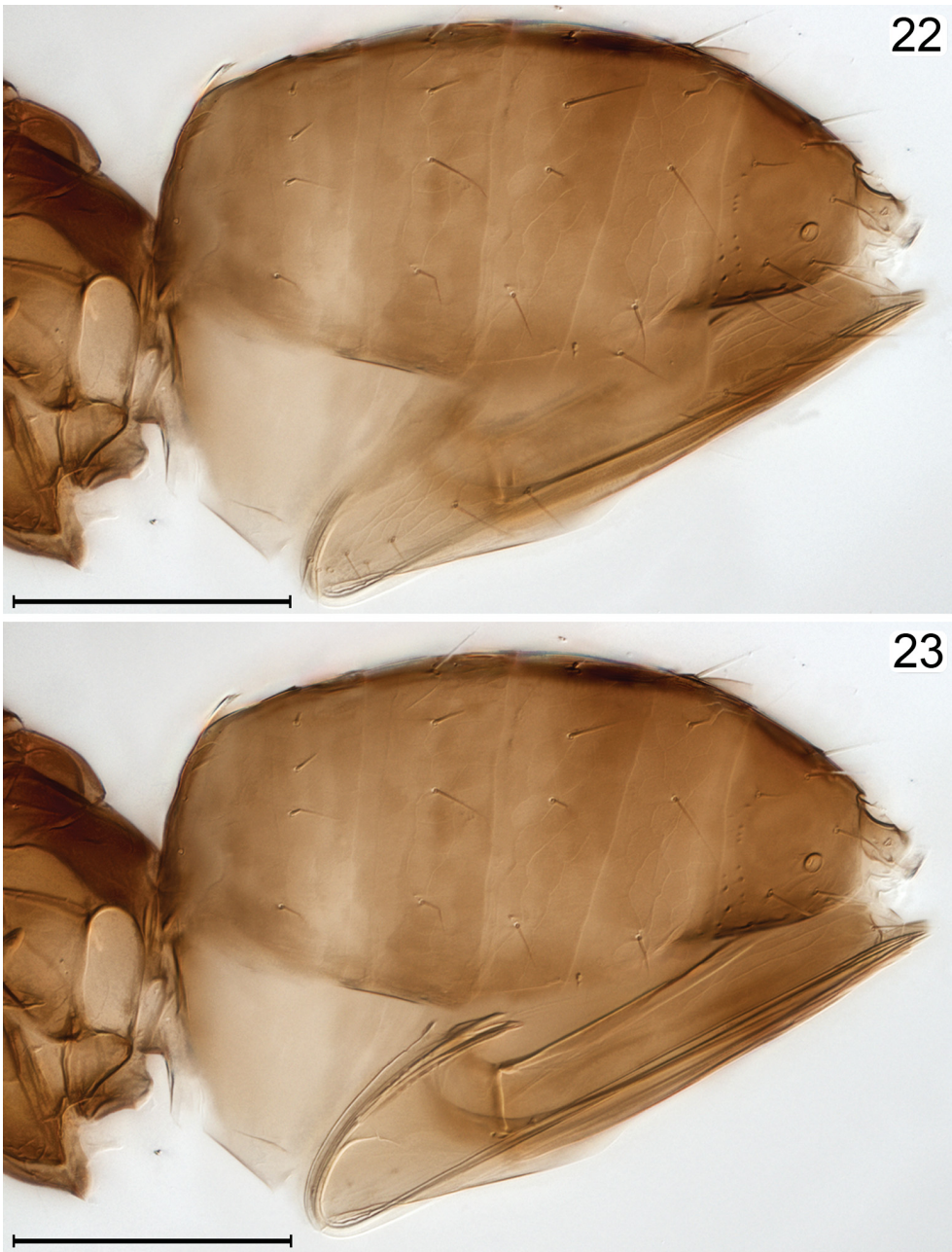
Figs 14–17. *Anaphes nipponicus* Kuwayama, 1932. 14 – female head, anterior view, scape and pedicel; 15 – female antenna, scape to fl_6; 16 – male head, posterior view; 17 – male antenna. Scale bars: 100 µm.



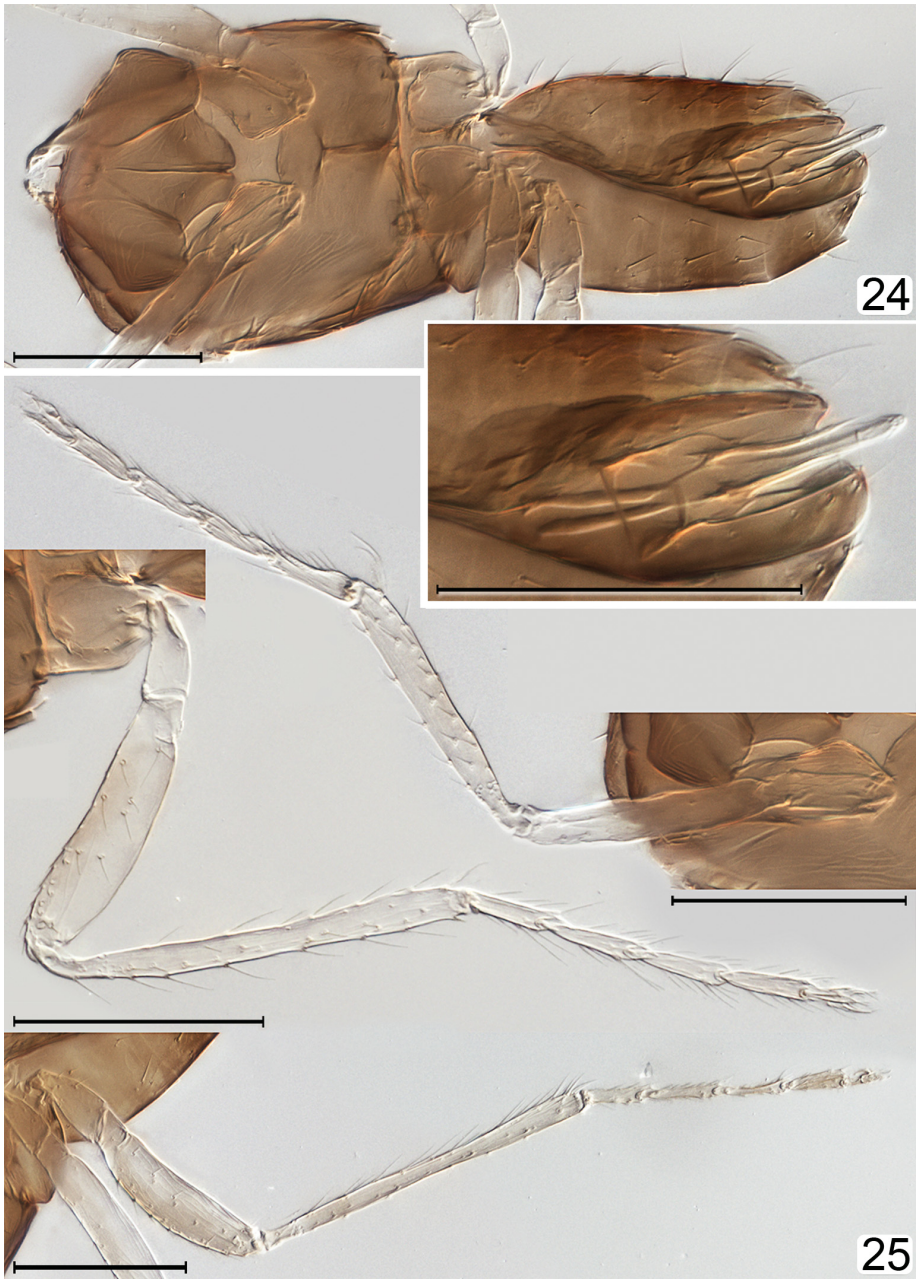
Figs 18–19. *Anaphes nipponicus* Kuwayama, 1932. 18 – female mesosoma, dorsal view; 19 – male wings. Scale bars: 100 µm.



Figs 20–21. *Anaphes nipponicus* Kuwayama, 1932, female metasoma. 20 – dorsal surface; 21 – dorsal view, showing genitalia through gaster. Scale bars: 100 μm.



Figs 22–23. *Anaphes nipponicus* Kuwayama, 1932, female metasoma, lateral view. 22 – left surface; 23 – more median view, showing genitalia. Scale bars: 100 μm.



Figs 24–25. *Anaphes nipponicus* Kuwayama, 1932, male. 24 – habitus, ventral view (inset shows genitalia enlarged); 25 – legs with left fore leg (upper image), right mid leg (middle image), left hind leg (lower image). Scale bars: 100 μm.

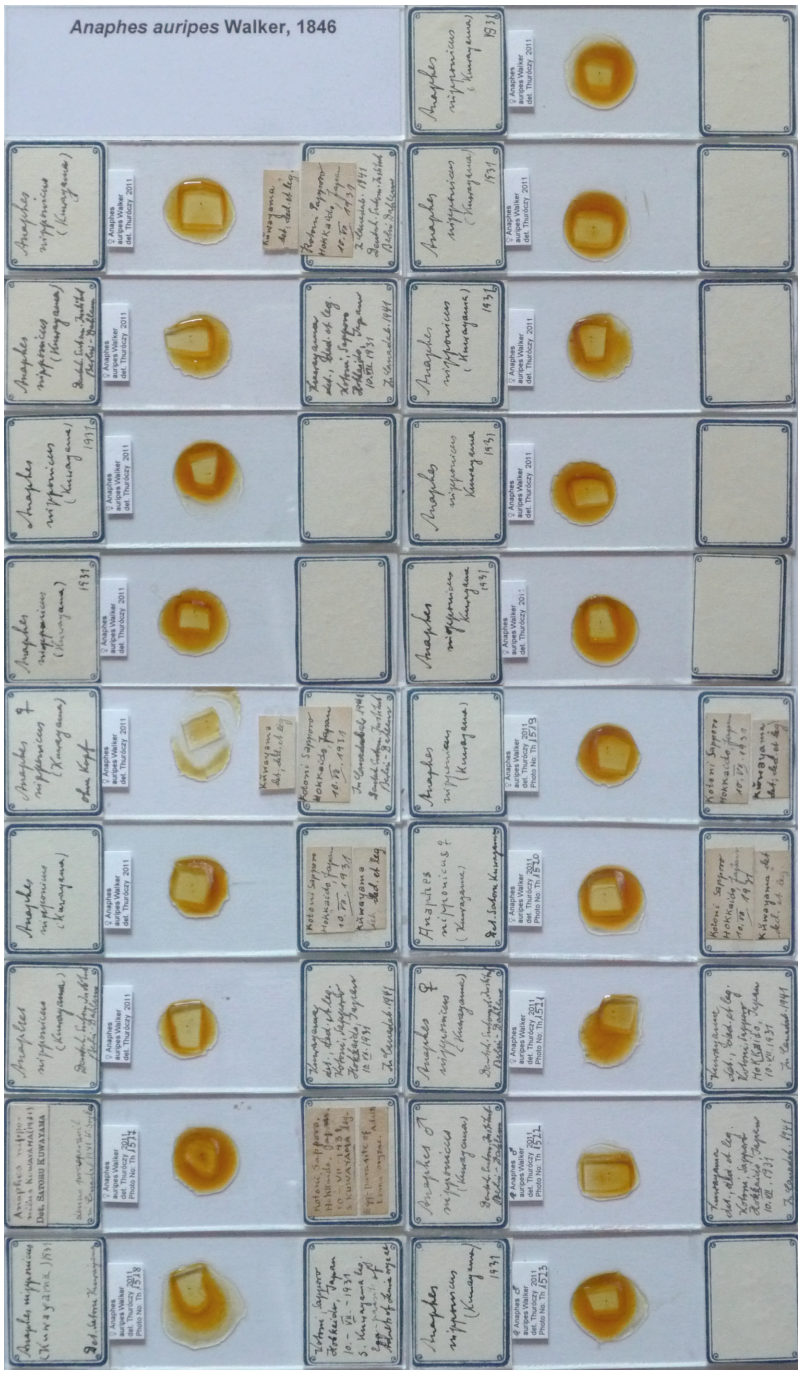


Fig. 26. *Anaphes nipponicus* Kuwayama, 1932, nineteen slides deposited in SDEI.

Redescription. ***Female.*** Body length [from original description] averaging 608. Colour. Body uniformly dark brown (Figs 18, 20–24) (shiny black in original description; the card-mounted specimens examined here were faded, and maceration in KOH to prepare slides made the colour even lighter); scape except radicle and pedicel laterally and ventrally yellowish. Head width 224 and 227 (n = 2), with occipital groove straight, almost parallel to posterior margin of eye. Head width 226 (Fig. 14). Antenna. Length/width (ratio) of segments (n = 1): scape (including radicle) 103/22 (4.6), pedicel 38/23 (1.7), fl_1 18/12 (1.5), fl_2 38/14 (2.7), fl_3 60/14 (4.3), fl_4 58/15 (3.9), fl_5 57/18 (3.2), fl_6 56/21 (2.7) (Fig. 15), clava missing but probably about 125/30 (4.2) [estimate based on the original description – 'club the longest, somewhat spindle-shaped, a little shorter than the last two funicle-joints combined, its width being a little slenderer than twice as wide as the last funicle-joint' – and photograph]; fl_3–fl_6 each with 2 mps. Mesosoma. Midlobe of mesoscutum with sculpure in concentric semicircles except posteromedially and frenum with sculpture in straight longitudinal lines (Fig. 18, male). Scutellum with campaniform sensilla separated by 2.3× diameter of sensillum. Wings. Fore wing missing; hind wing length 706, width 24, longest marginal setae 120. Legs. Metatibia length 245, metatasomere 1 0.75× length of metatarsomere 2. Metasoma. Gaster in dorsal view fairly short, with rounded apex (Figs 20, 21). Ovipositor length 247 (n = 1), not extending anteriorly under mesosoma (Figs 22, 23); OI 1.01.

Male. Leg colour light yellow except coxae brown and meso- and metafemora dorsally with brown suffusion (Fig. 24, cleared in KOH). Body length [from original description] averaging 496. Head width 185 (Figs 16). Antenna (Fig. 17): Length/width (ratio) of segments (n = 1): scape (including radicle) 85/24 (3.5), pedicel 40/28 (1.4), fl_1 4/9 (0.4), fl_2 60/23 (2.6), fl_3 66/19 (3.5), fl_4 66/21 (3.1), fl_5 68/21 (3.2), fl_6 65/21 (3.1), fl_7 66/22 (3.0), fl_8 57/22 (2.7), fl_9 63/22 (2.9), fl_{10} 56/20 (2.8), fl_{11} 63/20 (3.2); fl_6 with 4 mps. Total flagellum length 634. Wings. Fore wing with distinct brown tinge except for a narrow longitudinal area distal to medial space (Fig. 19); length 604, width 91, length/width 6.6; longest marginal setae about 104, marginal space length about 96, with single line of setae separating marginal space from hind margin. Hind wing with slight brown tinge; length 598, width 26, length/width 23.0, longest marginal setae about 112. Legs. Metatarsomere 1 0.7× as long as metatarsomere 2 (Fig. 25, bottom image). Metasoma. Genitalia in ventral view (Fig. 24).

Host. The only known host for *A. nipponicus* is the rice leaf beetle, *Oulema oryzae* (Chrysomelidae), an important pest of rice in parts of Asia.

Distribution. Palearctic Region: China (Roberts 2016), Japan (Hirashima 1989), Russia (Storozheva 1989), Taiwan (Thompson 1958).

Remark. Morphologically and biologically *A. nipponicus* appears to be the most similar species to *A. flavipes*. Whether *A. nipponicus* should be maintained as separate species needs further study, preferable using molecular evidence and, if laboratory colonies can be initiated and maintained, by conducting crossing experiments with *A. flavipes*.

Ackowledgements

Kazuaki Kamijo (retired in Bibai, Hokkaido, Japan), kindly sent JTH four specimens of *A. nipponicus* for study. S. Yoshimatsu (NIAES, Tsukuba) searched for the types of *A. nipponicus* but has not yet found them. We would like to thank Jitka Vilímová and David Král for transla-

tion of some Russian papers, Alena Kutíková for gathering some papers and Vanda Janštová for helping with the plotting of bar graphs. We thank Csaba Thuróczy (Köszeg, Hungary) for the image of all slides of *A. nipponicus* in SDEI. The photographs were expertly prepared by Jennifer Read and Lisa Bartels. The study was supported by grant GAUK 394415 (to AS), SVV 260434/2017 (to AS and PJ) and UNCE of Charles University no. 2014016 (to PJ).

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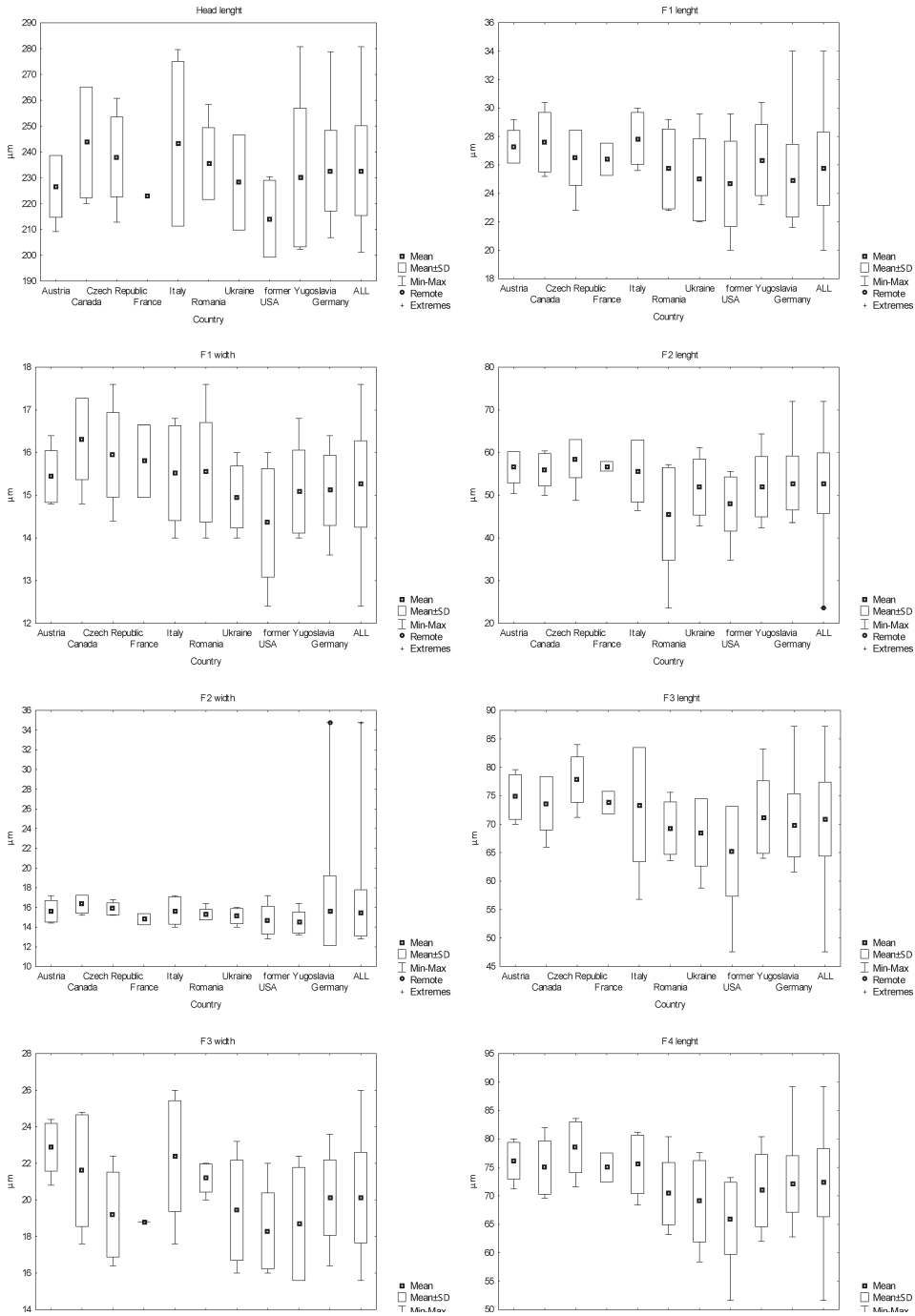
Appendix

Appendix 1. Measurements (in µm) including ratios for particular pair of measurement values of 89 females of *Anaphes flavipes* (Foerster. 1841) used in this study, showing minimum, maximum and median and mean including standard deviation values for each character/ratio (Fl = funicle segment).

	Min	Max	Median	Mean	SD
Head width	201	281	230	233	17
Fl1 length	20	34	26	26	3
Fl1 width	12	18	15	15	1
Fl1 length/width	1.3	2.4	1.7	1.7	0.2
Fl2 length	24	72	53	53	7
Fl2 width	13	35	15	15	2
Fl2 length/width	1.4	4.3	3.5	3.5	0.5
Fl3 length	48	87	72	71	6
Fl3 width	16	26	21	20	2
Fl3 length/width	2.8	4.6	3.4	3.6	0.4
Fl4 length	52	89	72	72	6
Fl4 width	16	28	21	21	3
Fl4 length/width	2.9	4.6	3.4	3.5	0.4
Fl5 length	52	87	72	72	5
Fl5 width	15	30	21	21	3
Fl5 length/width	2.6	4.6	3.4	3.5	0.5
Fl6 length	52	85	69	70	5
Fl6 width	17	28	22	22	3
Fl6 length/width	2.4	4.4	3.2	3.2	0.4
Clava length	107	151	129	129	8
Clava width	26	42	32	33	2
Clava length/width	3.2	4.8	3.9	4.0	0.3
Total flagellum length	405	605	493	494	35
Fore wing length	529	821	698	700	54
Fore wing width	69	145	98	100	12
Fore wing length/width	5.5	8.5	7.1	7.0	0.4
Metatibia length	175	310	239	238	23
Ovipositor length	200	309	262	261	19
Ovipositor index	0.9	1.4	1.1	1.1	0.1

Appendix 2. Measurements (in μm) including ratios for particular pair of measurement values of 10 males of *Anaphes flavipes* (Foerster. 1841) used in this study, showing minimum, maximum and median and mean including standard deviation values for each character/ratio (Fl = flagellar segment).

	Min	Max	Median	Mean	SD
Head width	185	228	198	200	14
Pedicel length	37	48	42	42	3
Pedicel width	23	33	28	29	3
Pedicel length/width	1.3	1.7	1.5	1.5	0.1
Fl1+Fl2 length	58	88	70	71	8
Fl1+Fl2 width	17	22	20	20	1
Fl1+Fl2 length/width	2.7	4.4	3.5	3.6	0.5
Fl3 length	58	82	68	69	7
Fl3 width	17	22	20	20	2
Fl3 length/width	2.9	4.2	3.5	3.5	0.4
Fl4 length	62	80	69	70	5
Fl4 width	17	22	20	20	1
Fl4 length/width	3.1	4.2	3.5	3.6	0.4
Fl5 length	62	82	70	71	6
Fl5 width	17	22	20	20	1
Fl5 length/width	3.1	4.1	3.6	3.7	0.3
Fl6 length	60	82	70	71	6
Fl6 width	17	22	19	19	1
Fl6 length/width	3.0	4.2	3.8	3.7	0.3
Fl7 length	58	83	68	70	7
Fl7 width	17	22	20	20	2
Fl7 length/width	2.9	4.1	3.5	3.5	0.3
Fl8 length	57	82	69	70	7
Fl8 width	17	23	19	20	2
Fl8 length/width	3.1	4.1	3.6	3.6	0.3
Fl9 length	57	80	70	70	7
Fl9 width	17	23	20	21	2
Fl9 length/width	2.8	4.2	3.5	3.5	0.4
Fl10 length	55	82	69	69	7
Fl10 width	18	23	20	20	2
Fl10 length/width	2.8	3.8	3.5	3.5	0.3
Fl11 length	63	82	73	74	5
Fl11 width	17	22	19	19	2
Fl11 length/width	3.5	4.4	3.9	3.9	0.4
Total flagellum length	590	815	698	706	64
Fore wing length	640	840	715	724	63
Fore wing width	85	118	104	102	13
Fore wing length/width	6.1	7.8	7.2	7.1	0.5
Hind wing length	590	770	665	678	61
Hind wing width	25	33	30	30	4
Hind wing length/width	19.8	24.8	22.6	22.3	1.9
Metatibia length	200	270	225	226	21


Head lenght
F1 lenght
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F2 lenght
F2 width
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µm
Austria
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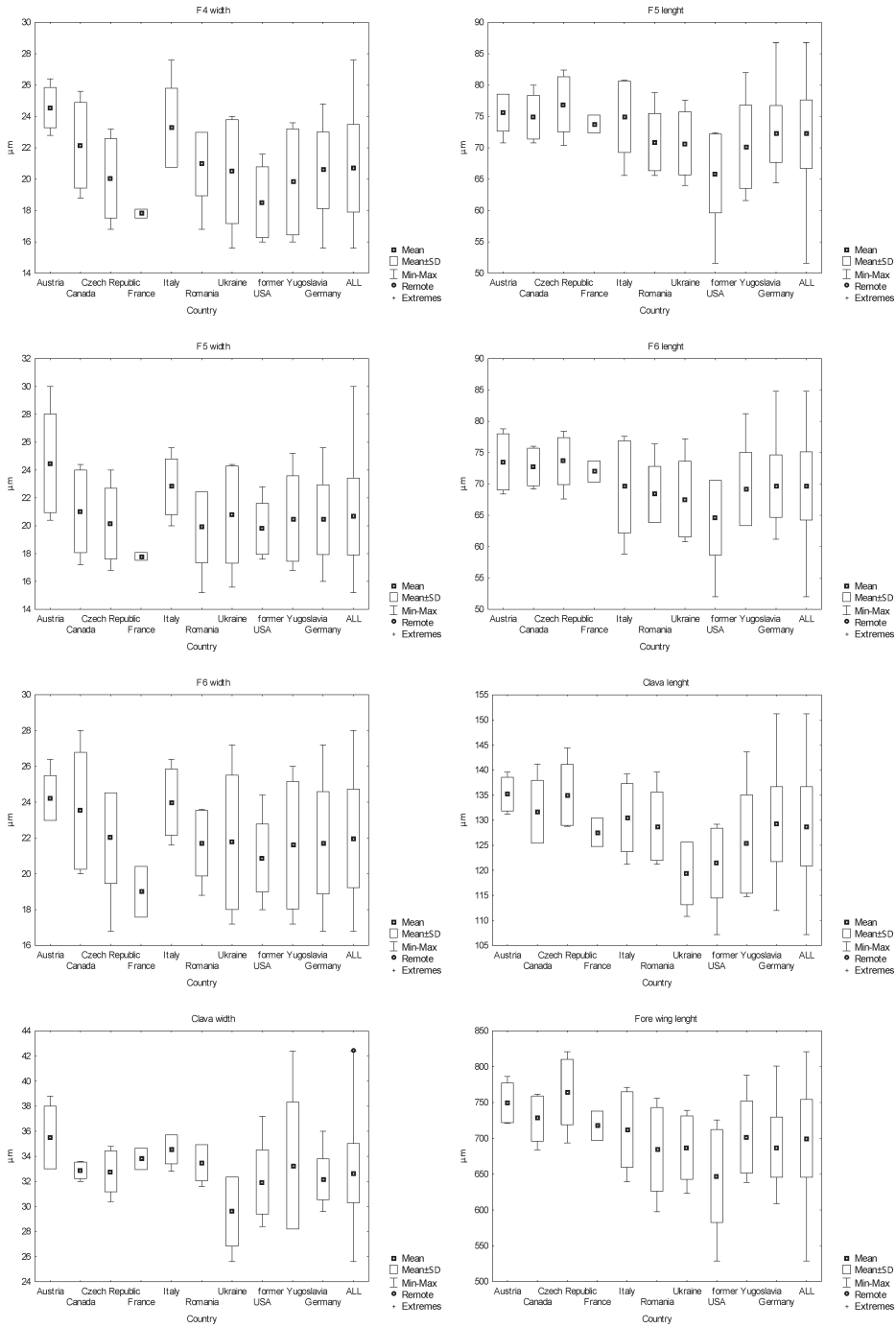
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Clava lenght
Clava width
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Austria
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Czech Republic
France
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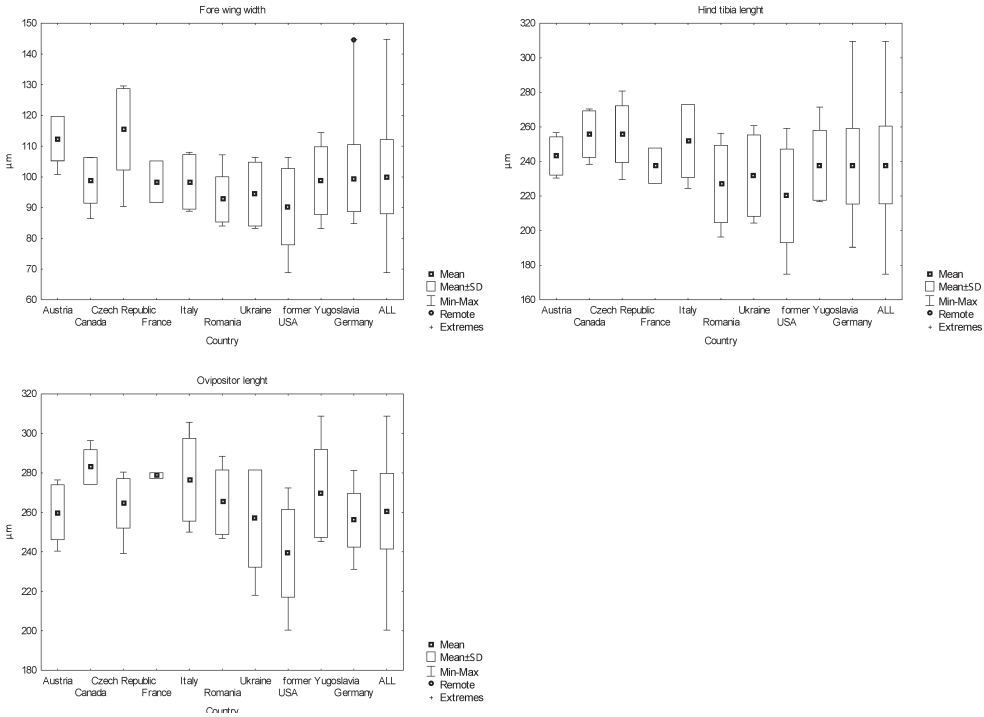

Appendix 3 (on two previous and this page). Bar plots of all measurements (in µm) of 89 females of Anaphes flavipes (Foerster, 1841) used in this study showing minimum, maximum and mean including standard deviation, remote and extreme values for each character grouped according to countries of origin and all countries together (ALL).