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REVIEW OF HERB GALL WASP TRIBES (HYMENOPTERA: CYNIPIDAE: AYLACINI *SENSU LATO*), WITH AN UPDATED KEY TO CYNIPID TRIBES AND A CHECKLIST OF WORLD SPECIES

Louis F. Nastasi, Charles K. Davis, José Luis Nieves-Aldrey, Matthew L. Buffington, Simon Van Noort, and Andrew R. Deans

(LFN) Frost Entomological Museum, Department of Entomology, The Pennsylvania State University, University Park, PA, USA, 16802 (email: lfnastasi@gmail.com, https://orcid.org/0000-0001-7825-480X); (CKD) Frost Entomological Museum, Department of Entomology, The Pennsylvania State University, University Park, PA, USA, 16802 (email: ckd5093@psu.edu, https://orcid.org/0000-0001-6056-3903); (JLNA) Departamento de Biodiversidad y Biología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain (email: aldrey@mncn.csic.es, https://orcid.org/0000-0002-4711-7455); (MLB) Systematic Entomology Laboratory, USDA-ARS, c/o National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (email: matt.buffington@usda.gov, https://orcid.org/0000-0003-1900-3861); (SvN) Research and Exhibitions Department, South African Museum, Iziko Museums of South Africa, Cape Town, South Africa (email: svannoort@iziko.org.za, https://orcid.org/0000-0001-6930-9741); (ARD) Frost Entomological Museum, Department of Entomology, The Pennsylvania State University, University Park, Pennsylvania, USA (email: ard19@psu.edu, https://orcid.org/0000-0002-2119-4663).

Abstract.—We review the tribes of Cynipidae that are known to contain gall inducers on herbaceous plants, which are presently classified in four tribes: Aulacideini, Aylacini, Diastrophini, and Phanacidini. We provide a revised key to these tribes, diagnostic characters for each tribe, and an updated key to brachypterous and apterous Cynipoidea including the inclusion of brachyptery in Phanacidini. We propose the replacement name *Eubothrus* Förster, 1869 for the genus *Isocolus* Förster, 1869 (Aulacideini) as the latter is a homonym of the trilobite genus *Isocolus* Angelin, 1854 (Trilobita: Isocolidae). We also provide a checklist of world herb gall wasp species including host plant and geographic distribution data. Overall, we report 166 species of herb gall wasps, finding 96 species in 11 genera in Aulacideini, 6 species in 3 genera in Aylacini, and 39 species in 4 genera in Phanacidini, as well as 25 gall-inducing species in 3 genera in Diastrophini, of which 11 are or probably are associated with herbaceous plants. Online Lucid identification keys and images of all the taxa treated herein are available at: **http://www.waspweb.org**.

Key Words: Aulacideini, Diastrophini, identification key, Phanacidini, taxonomy.

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Gall wasps (Hymenoptera: Cynipoidea: Cynipidae *sensu lato*) comprise a diverse lineage of phytophagous hymenopterans that induce galls to shelter and nourish their progeny (Ronquist and Liljeblad 2001, Melika 2006, Buffington et al. 2020). While many cynipid studies focus on familiar taxa associated with oaks (Fagaceae: *Quercus* L.), gall wasps associated with herbaceous plants are also diverse, compelling, and increasingly the subject of diverse research (e.g., Buffington et al. 2017, Tavakoli et al. 2022, Nieves-Aldrey 2022, Nastasi et al. 2024d). Cynipids associated with herbaceous plants were previously classified in a single tribe, Aylacini Ashmead, 1903 but were recently reclassified into four tribes (Figs. 1–4): *Aylacini sensu stricto;* Aulacideini Nieves-Aldrey, Nylander, and Ronquist, 2015; Diastrophini Nieves-Aldrey, Nylander, and Ronquist, 2015; and Phanacidini Nieves-Aldrey, Nylander, and Ronquist, 2015 (Ronquist et al. 2015, Buffington et al. 2020). Of these four tribes, three (Aylacini, Aulacideini, and Phanacidini) exclusively include gall-inducing species, while Diastrophini includes both gall inducers and inquilines of cynipid galls (Ronquist et al. 2015, Buffington et al. 2020, Nastasi et al. 2024b).

Figs. 1–4. Cynipid galls on herbaceous plants. Asteraceae: 1, Gall of *Phanacis hypochoeridis* (Phanacidini) on *Hypochaeris radicata*, photographed by Cricket Raspet, licensed via CC BY-NC 4.0. Lamiaceae: 2, Gall of *Liposthenes glechomae* (Aulacideini) on *Glechoma hederacea*, photographed by emendela, licensed via CC BY-NC 4.0. Papaveraceae: 3, Gall of *Aylax papaveris* (Aylacini) on *Papaver* sp., photographed by Faluke Luke, licensed via CC BY-NC 4.0. Rosaceae: 4, Gall of *Diastrophus potentillae* (Diastrophini) on *Potentilla simplex*, photographed by Charles Davis.

Species in the herb-galling tribes in particular are of growing interest, due in part to their potential applications in biocontrol, their developing roles as agricultural pests, and in broader studies of gall wasp evolution (Ronquist et al. 2015, Buffington et al. 2017, Buffington et al. 2020, Nastasi et al. 2024c, 2024d). However, the world fauna of these tribes has not recently been cataloged, and keys to higher cynipoid taxa, while generally excellent, do not accurately route some herb-galling species. As a result, to better enable further research on herb gall wasps, a taxonomic review including an updated checklist and revised keys to the tribes is warranted.

Materials and Methods

Morphology follows the Hymenoptera Anatomy Ontology (Yoder et al. 2010) and the Phenotype and Trait Ontology (PATO Curators 2023). Gall phenotype terminology follows GallOnt (Deans et al. 2024). Those unfamiliar with cynipoid morphology should also consult Goulet and Huber (1993) and Melika (2006). We imaged specimens using a Macroscopic Solutions 'microkit' (Tolland, Connecticut, USA). We stacked images using Zerene Stacker LLC version 1.04 (Richland, Washington, USA), and edited images using Adobe Photoshop and Illustrator (San Jose, California, USA).

The Lucid identification keys available on WaspWeb (van Noort, 2024) and published in Buffington et al. (2020) were updated according to our latest taxonomic concepts and character assessments. Lucid pathway and Lucid matrix keys were developed using Lucid Builder version 4.0.38. Character matrices were generated and edited using Microsoft Excel; matrices were then used as input into Lucid matrix key production (Penev et al., 2009). The online interactive keys were produced using Lucid meeting the requirements of publishing both static and dynamic interactive keys under an open access model (Penev et al., 2009). All keys were illustrated using high quality annotated images, highlighting diagnostic characters. The images are integrated into the key above each couplet resulting in a user-friendly output. This key format reduces the requirement of familiarity with morphological terminology associated with a particular taxonomic group, because the characters are visually illustrated making the keys usable by a wide range of end-users including ecologists and conservationists. Online identification keys are presented in two different formats on WaspWeb: traditional static dichotomous keys where a choice needs to be made at each key couplet to continue, which are also presented as an interactive Lucid pathway (dichotomous) key; and Lucid matrix keys where relevant states from multiple character features can be selected independently until identification is achieved. For more information concerning Lucid keys visit https://www.lucidcentral.org.

We referenced specimens housed in the following institutions:

AMNH: American Museum of Natural History, New York, New York, USA

CNC: Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada

EMEC: Essig Museum of Entomology, University of California, Berkeley, California, USA

EMUS: Entomology Museum of Utah State, Utah State University, Logan, Utah, USA

INHS: Illinois Natural History Survey, University of Illinois, Champaign, Illinois, USA

MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain

PSUC: Frost Entomological Museum, The Pennsylvania State University, University Park, Pennsylvania, USA

USNM: United States National Museum, Washington, D.C., USA

RESULTS

Buffington et al. (2020) keyed the higher taxa of Cynipoidea; however, our continuing work on herb gall wasps has found character states that are not represented in the key. Aulacideini keys to couplet 16, where it is differentiated from Aylacini by the striate sculpture of the mesopleuron and the number of flagellomeres in females, among other characters. However, Aulacideini may have several different sculpture patterns on the mesopleuron, and females of some species can have 12 flagellomeres as in Aylacini. We also find that the description of the pronotal pits for Aylacini in couplet 16 falls within the range of variation seen in Aulacideini. These characters prevent many herb gall wasps, especially Nearctic aulacideines, from being conveniently and reliably identified. Additionally, many Diastrophini exhibit conspicuous sculpture on the mesosoma, thus appearing matte rather than smooth as suggested in the key. Addressing this, we provide an updated key to the tribes of herb-galling Cynipidae; these replace couplets 14 through 16 in Buffington et al. (2020) as indicated by the couplet numbering. We also provide an updated matrix key to the tribes of Cynipidae sensu lato, available at [https://www.waspweb.org/Cynipoidea/Keys/Lucid_Matrix_keys/World_tribes_Cynipidae_2024/cynipidae_world_tribes_lucid_matrix_key_2024.html]. While the inquiline species of Diastrophini are not discussed further in this study, all species of Diastrophini will correctly route in the below key, although inquilines are directed to other paths in the key given by Buffington et al. (2020).

To further establish the identities of the herb galling tribes, we provide taxon treatments for each tribe, including morphological diagnoses, overviews of host plant associations, and updated distributions. We also provide an updated species checklist, finding 166 species of herb gall wasps in 21 genera across the four tribes.

Key to the World Tribes of Herb-galling Cynipoidea

1 (14) Pronotal plate complete, with edges reaching the anterior mesoscutum and forming plate conspicuously raised above rest of pronotum (Figs. 5–6, paired arrows indicate margins of pronotal plate). Metatarsal claws with conspicuous basal lobes (Figs. 9–11, arrow). Gall inducers or inquilines on Rosaceae ..... Diastrophini

— Pronotal plate incomplete, well-defined only ventrally and with edges not conspicuously reaching anterior mesoscutum (Figs. 7–8, paired arrows indicate margins of pronotal plate). Metatarsal claws simple, without conspicuous lobes (Figs. 12–14). Gall inducers on other families 2 (15)

2 (15) Pronotum in dorsal view short, with medial height about 1/5 as long as outer lateral margin (Fig. 15–16). Antennae always 14-segmented in females and 15-segmented in males. Fore wing always with conspicuous areolet (Fig. 19) and always with marginal cell open (Fig. 19). Gall inducers on *Papaver* (Papaveraceae) only. Palearctic only ..... Aylacini

— Pronotum in dorsal view long, with medial height about 1/4 to 1/3 as long as outer lateral margin (Figs. 17–18). Antennae 12-, 13-, or 14-segmented in females and 13- or 14-segmented in males. Fore wing with (Fig. 21) or without areolet (Fig. 20), and with marginal cell open (Fig. 20), closed (Fig. 21), or partially closed (Fig. 22). Gall inducers on herbs other than *Papaver*, primarily Asteraceae and Lamiaceae but more rarely on other families (including Papaveraceae). Palearctic or Nearctic 3 (16)

3 (16) Pronotal submedial pits shallow and effaced, apparent as a continuous

Figs. 5–8. Pronotal plates. Scale bars: 0.25 mm. Paired arrows indicate extent of defined area of pronotal plate. 5, *Diastrophus* sp. (PSUC_FEM_246198), anterior pronotum. 6, *Diastrophus* sp. (USNMENT01448499), lateral pronotum. 7, *Aulacidea tumida* (PSUC_FEM_253277), anterior pronotum. 8, *Antistrophus pisum* (PSUC_FEM_247264), anterior pronotum.

transverse medial impression (Figs. 23–24, arrow). Marginal cell usually partially closed, with vein R1 reaching and continuing along anterior wing margin but terminating long before reaching vein Rs (Fig. 22); rarely entirely open or entirely closed ..... Phanacidini

— Pronotal submedial pits deep and apparent as a pair of conspicuous ovate impressions (Figs. 25–26, arrows). Marginal cell always either entirely open, without vein R1 conspicuously continuing along wing margin (Fig. 20), or entirely closed (Fig. 21) ..... Aulacideini

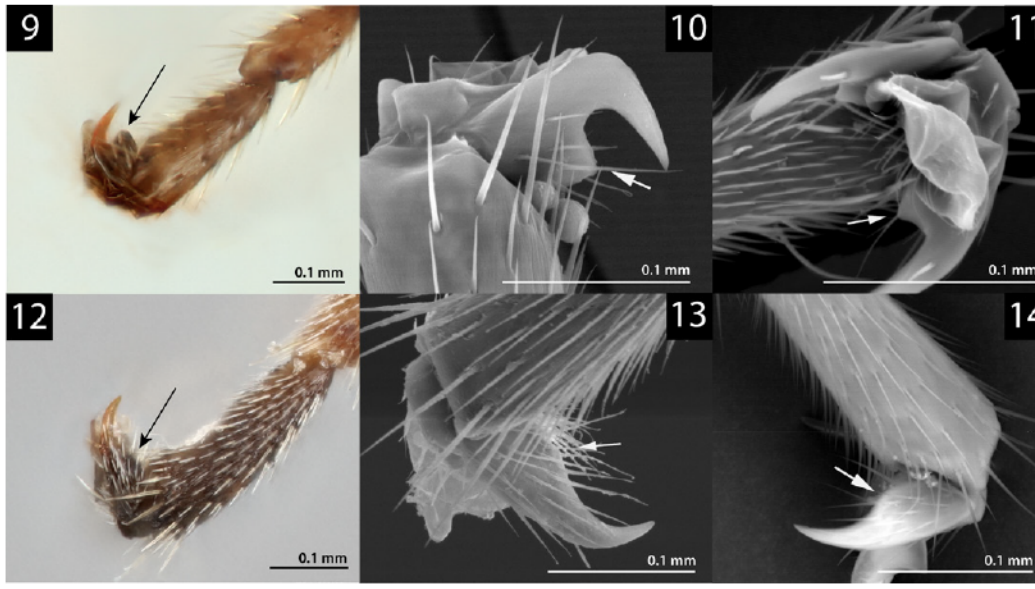
Additionally, males of at least one herb gall wasp species, *Phanacis centaureae* Förster, 1860 (Fig. 34), are brachypterous (Nieves-Aldrey 2001, Melika 2006). If male *P. centaureae* are keyed through couplet 33 in Buffington et al. (2020), where brachypterous or apterous specimens are routed, they would be incorrectly identified as the figitid subfamily Charipinae. To address this, we provide the below key to brachypterous and apterous cynipoids to replace couplets 33 and 34 in Buffington et al. (2020):

Key to apterous and brachypterous Cynipoidea

1 (33) Scutellum with raised ovate plate (Figs. 27–28, arrows) ..... Figitidae: Eucoilinae

— Scutellum without plate (Figs. 29–30) 2 (34)

2 (34) Pronotum dorsomedially short, around 1/7 as long as greatest length of



Figs. 9–14. Metatarsal claws; arrows indicate presence (Figs. 9–11) or absence (Figs. 12–14) of basal lobe. Scale bars: 0.05 mm. 9, *Diastrophus kincaidii* (PSUC_FEM_251280). 10, *Diastrophus rubi* (MNCN). 11, *Xestophanes potentillae* (MNCN). 12, *Antistrophus silphii* (CYNANT0048). 13, *Iraella hispanica* (MNCN). Figure 14. *Phanacis kiefferi* (MNCN).

pronotum laterally. Metasoma usually at least twice the size of the mesosoma (Fig. 31). Only females brachypterous or apterous .....Cynipidae: Cynipini

— Pronotum dorsomedially tall, at least 1/5 and usually 1/3 as long as greatest length of pronotum laterally. Metasoma about the size of the mesosoma (Figs. 32). Females or males brachypterous or apterous.....3 (35)

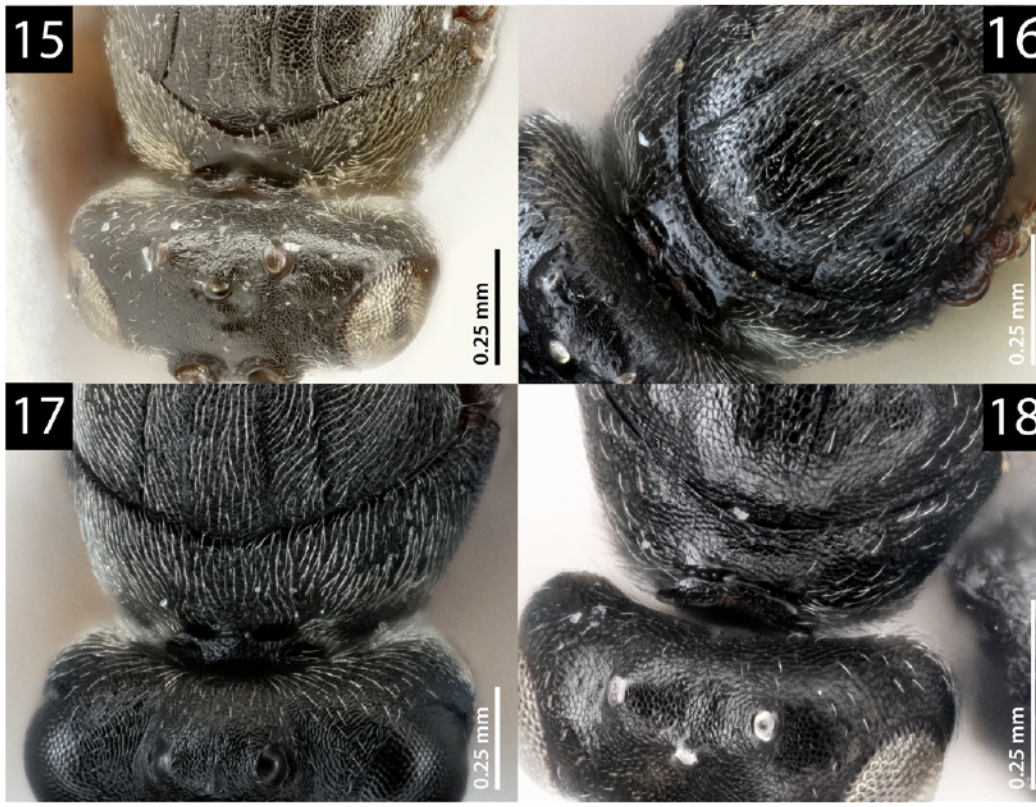
3 (35) Mesoscutellar foveae indistinct (Fig. 33). Base of metasoma usually with conspicuous setose patch (Figs. 32–33). Both sexes brachypterous or apterous..... .....Figitidae: Charipinae

— Mesoscutellar foveae conspicuously impressed (Fig. 34, arrow). Base of metasoma without abundant setae (Fig. 35). Only with brachypterous males (Fig. 36).....Cynipidae: Phanacidini

Tribes of herb-galling Cynipidae

Aulacideini Nieves-Aldrey, Nylander, and Ronquist, 2015

Diagnosis.—Pronotum in dorsal view long, with medial height about 1/4 to 1/3 as long as outer lateral margins (Figs. 17; 25–26). Pronotal plate short and incomplete, with lateral edges marked only for a short distance dorsally (Figs. 9–10; 25–26); rarely with lateral edges longer but never reaching mesoscutum or forming a conspicuous raised plate. Pronotal submedial pits conspicuous, apparent as a pair of ovate impressions (Figs. 25–26). Tarsal claws simple, without lobes (Fig. 13). Antennae with 12, 13, or 14 antennomeres in females and 13 or 14 antennomeres in males. Fore wing with (Fig. 21) or without areolet (Fig. 20), with marginal cell entirely open (Fig. 20) or entirely closed (Fig. 21). Galls on herbaceous plants other

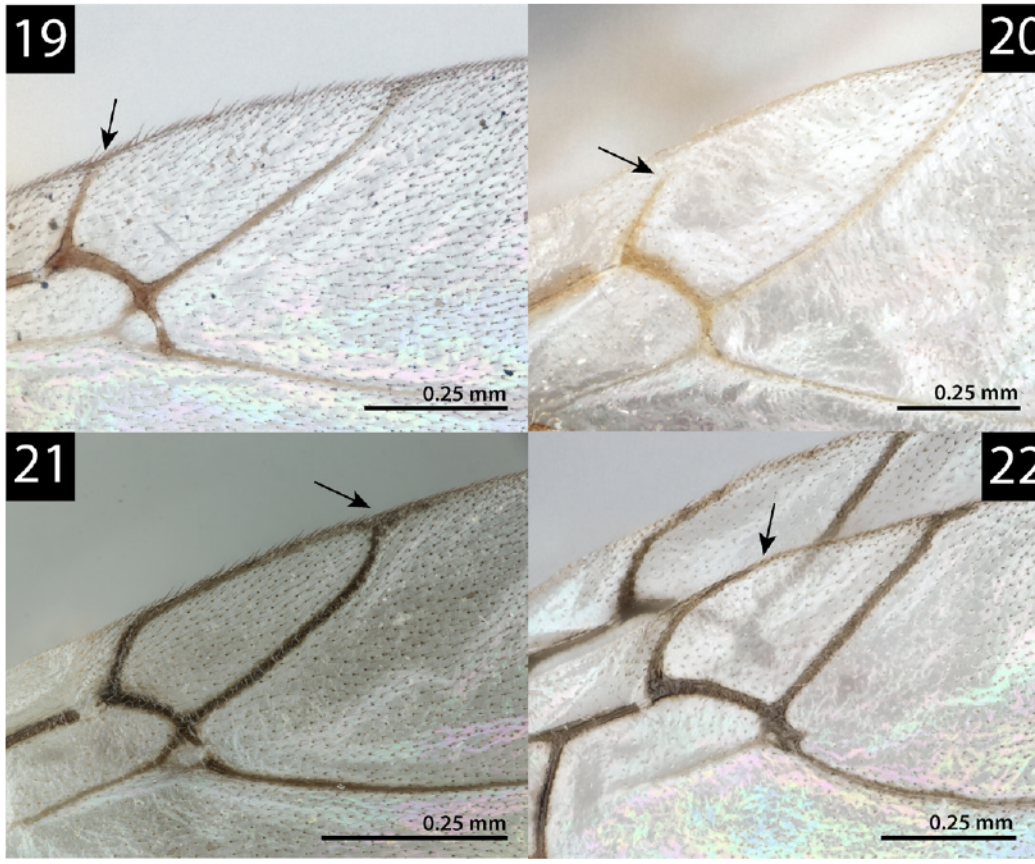


Figs. 15–18. Scale bars: 0.25 mm. 15, *Iraella ionescui* (USNMENT01231864), dorsal pronotum. 16, *Aylax papaveris* (AMNH_IZC 430600), dorsal pronotum. 17, *Aulacidea tumida* (PSUC_FEM_253277), dorsal pronotum. 18, *Phanacis hypochoeridis* (PSUC_FEM_271946), dorsal pronotum.

than Rosaceae or *Papaver* (Papaveraceae) (Figs. 49–57).

Biology.—Gall inducers on several plant families, with most species associated with Asteraceae and Lamiaceae. Species of Aulacideini induce galls on the stems, flowers, leaves, or roots of their host plants. Galls induced by Aulacideini can be cryptic or externally conspicuous. Known host genera are the following: Apiaceae(*)–*Eryngium* L.(*). Asteraceae–*Ambrosia* L.(*), *Arnica* L.(*), *Carthamus* L., *Centaurea* L., *Chartolepis* Cass., *Chrysothamnus* Nutt., *Cirsium* Mill., *Cousinia* Cass., *Echinops* L., *Hieracium* L., *Inula* L., *Koelpinia* Pall., *Lactuca* L., *Launaea* Cass., *Leuzea* DC., *Lygodesmia* D.Don, *Microseris* D.Don, *Nabalus* Cass., *Pilosella* Hill, *Rhaponticum* Ludw., *Saussurea* DC., *Scorzonera* L., *Serratula* L., *Silphium* L., *Silybum* Adans., *Sonchus* L., *Tragopogon* L. Caprifoliaceae–*Valeriana* L. Lamiaceae–*Glechoma* L., *Nepeta* L., *Phlomis* L., *Salvia* L. Papaveraceae–*Fumaria* L., *Hypecoum* L. Plantaginaceae(*)–*Digitalis* Tourn. Ex L.(*). Rosaceae(*)–*Rubus* L.(*). Suspect records are indicated by (*) following Nastasi and Deans (2021), Nastasi and Deans (2024a), and Nieves-Aldrey (2022). Known host records for each species are given in the below species checklist. We regard Asteraceae, Caprifoliaceae, Lamiaceae, and Papaveraceae as definite host family records.

Distribution.—Holarctic; most species known from western Europe, Russia, Ukraine, and North America, with additional records from the Middle East, Mongolia, and China



Figs. 19–22. Scale bars: 0.25 mm. Arrows indicate end of vein R1. 19, *Aylax minor* (INHS 288691), fore wing marginal cell. 20, *Antistrophus microseris* (EMEC 1131294), fore wing marginal cell. 21, *Aulacidea* sp. (PSUC_FEM_246286), fore wing marginal cell. 22, *Phanacis hypochoeridis* (PSUC_FEM_271946), fore wing marginal cell.

(Melika 2006, Nastasi and Deans 2021, 2024a, 2024c, Nieves-Aldrey 2022). Several species of *Aulacidea* have been introduced to New Zealand, the US, Canada, and possibly elsewhere for biological control of their host plants (Nastasi and Deans 2021, Nastasi et al. 2024b, Ward 2014). Palearctic species, especially those associated with *Salvia* L. (Lamiaceae), are occasionally intercepted at ports of entry to the United States (Buffington, pers. obs.). We have seen a female representing an undescribed genus from South Africa, suggesting that Aulacideini have a much broader distribution than currently known.

Included genera.—The following 11 genera are classified in Aulacideini: *Antistrophus* Walsh, 1869 (Figs. 37–38; 49); *Aulacidea* Ashmead, 1897 (Figs. 39–40; 50); *Cecconia* Kieffer, 1902; *Eubothrus* Förster, 1869 (=*Isocolus*; see remarks below; Figs. 41–42; 51); *Fumariphilus* Nieves-Aldrey, 2022 (Figs. 43; 52); *Hedickiana* Nieves-Aldrey, 1994 (Figs. 44; 53); *Liposthenes* Förster, 1869 (Figs. 2; 45; 57); *Neaylax* Nieves-Aldrey, 1994 (Figs. 46; 56); *Panteliella* Kieffer, 1901 (Figs. 47; 54); *Rhodus* Quinlan, 1968 (Figs. 48; 55); and *Soparia* Nastasi, 2024. An undescribed genus is known from Kenya (unpublished data).

Remarks.—Many taxa in Aulacideini require revision, especially *Aulacidea*, which is consistently retrieved in phylogenetic studies as polyphyletic (e.g., Ronquist et al. 2015). The

Figs. 23–26. Scale bars: 0.25 mm. Arrows indicate continuous pronotal impression (Figs. 23–24) or pronotal pits (Figs. 25–26). 23–24, *Phanacis hypochoeridis* (PSUC_FEM_271946), dorsal and dorsolateral pronotum. 25, *Antistrophus pisum* (PSUC_FEM_247264), anterodorsal pronotum. 26, *Antistrophus bicolor* (USNMENT 01448496), dorsolateral pronotum.

Western Palearctic fauna has been intensively studied in recent years, including descriptions of many new species and investigation of community structure (e.g., Askew et al. 2006, Nieves-Aldrey 1994a, 1994b, 1995, 2001, 2004, 2012, 2022). In contrast, the Nearctic fauna of Aulacideini has been largely unstudied in recent decades, excluding a single taxonomic study in 2004 (Tooker et al. 2004), although the Nearctic Aulacideini are currently under revision and several studies have reported findings from this initiative (Nastasi et al. 2024b, 2024c, 2024d, Nastasi and Davis 2022). The Nearctic and Western Palearctic genera are currently under revision including new data from phylogenomic analysis (Nastasi, Nieves-Aldrey, et al., unpublished data).

The Eastern Palearctic fauna has been found to be quite diverse but has been less studied. Many Eastern Palearctic species require further revision, especially those authored by Diakontschuk (e.g., Diakontschuk 1988), given interesting morphology and host use in these species (Melika 2006; see host records in below checklist).

Further, the generic name *Isocolus* Förster, 1869 is evidently a junior homonym of *Isocolus* Angelin, 1854 (Trilobitomorpha: Isocolidae) and thus in need of replacement. We apply *Eubothrus* Förster, 1869 as a replacement name for *Isocolus*, following Article 60.2 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999). *Eubothrus*

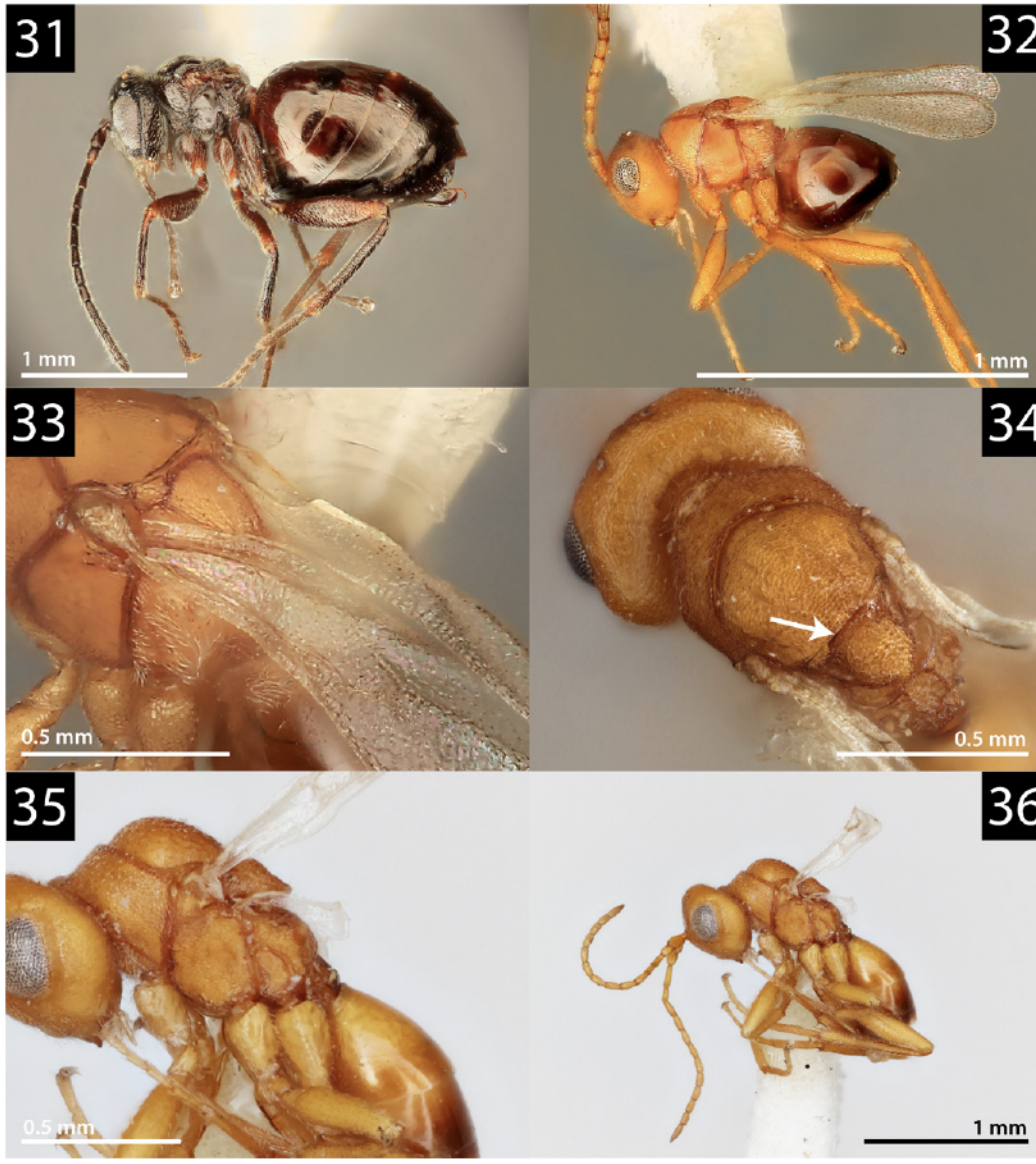
Figs. 27–30. Brachypterous and apterous Cynipoidea. Scale bars: 0.25 mm. Figure 27. *Kleidotoma* sp. (USNMENT0152865), dorsolateral scutellum; arrow indicates scutellar plate. Figure 28. *Striatovertex* sp. (USNMENT01271830), dorsal scutellum; arrow indicates scutellar plate. Figure 29. *Phylloteras* sp. (USNMENT01231835), dorsal scutellum. Figure 30. *Lytoxysta brevipalpis* (USNMENT1231836), dorsal scutellum.

is the earliest junior synonym of *Isocolus* and was described in the same paper as *Isocolus* and using the same type species (*Diastrophus scabiosae* Girault, 1859) (Förster, 1869). New combinations in *Eubothrus* for all species presently placed in *Isocolus* are given in our below checklist.

Lastly, during another study on Aulacideini, we corresponded with the Natural History Museum of Denmark regarding the type material of *Aulacidea arnicae* Hoffmeyer, 1930, a species supposedly inducing galls on *Arnica* spp. (Asteraceae). The type material, which comprised a holotype female and paratype male, were originally deposited there, but have both been lost since at least 1991 (L. Vilhelmsen, pers. comm.). To avoid including taxa of dubious status in our checklist, we here consider *Aulacidea arnicae* to be a *nomen dubium* on the basis of the missing type material. Examination of the type material, if located, will be critical in establishing the identity of this species; an association with *Arnica* L. (Asteraceae) is rather suspect, as no other cynipoid wasp is known in association with the tribe Madieae.

Aylacini Ashmead, 1903

Diagnosis.—Pronotum in dorsal view somewhat short, with medial height about 1/5 as long as outer lateral margins (Figs. 15–16). Pronotal plate short and incomplete, with lateral edges marked only for a short distance dorsally (Figs. 15–16). Pronotal submedial pits conspicuous, apparent as a pair of ovate impressions (Figs. 15–16). Tarsal claws simple, without lobes (Fig. 13). Antennae with 14 antennomeres in females and 15 antennomeres in males. Fore wing (Fig. 19) always with areolet and with marginal cell entirely open.

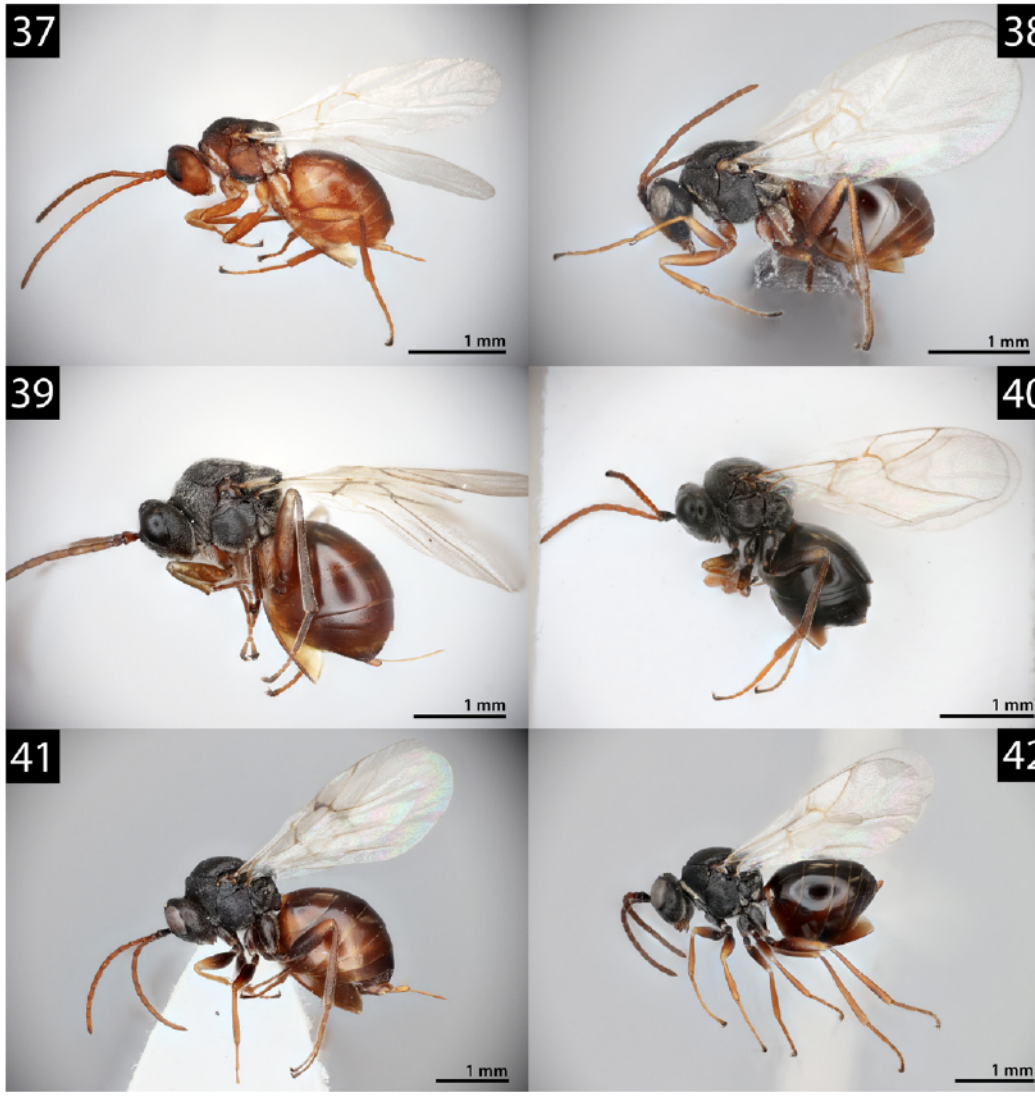


Figs. 31–36. Brachypterous and apterous Cynipoidea. 31, *Phylloteras* sp. (USNMENT 01231835), lateral habitus. 32. *Lytoxysta brevipalpis* (USNMENT01231836), lateral habitus. 33, *Lytoxysta brevipalpis* (USNMENT 01231836), dorsolateral mesosoma. 34, *Phanacis centaureae* (USNMENT 01823221), dorsal mesosoma. 35, *Phanacis centaureae* (USNMENT 01823221), lateral mesosoma. 36, *Phanacis centaureae* (USNMENT 01823221), lateral habitus.

Galls exclusively on *Papaver* (Papaveraceae) (Figs. 63–65).

Biology.—All species of Aylacini induce galls on several species of *Papaver* L. (Papaveraceae), most commonly *P. dubium* L., *P. rhoeas* L., and *P. somniferum* L. (Nieves-Aldrey 1994b, 2005, Melika 2006, Pujade-Villar and Schiopu 2015).

Distribution.—Palearctic; widespread throughout and found throughout Europe,



Figs. 37–42. Aulacideini adult female lateral habiti. 37, *Antistrophus meganae* (PSUC_FEM_247327). 38, *Antistrophus microseris* (EMEC 1131294). 39, *Aulacidea tumida* (PSUC_FEM_253277). 40, *Aulacidea acroptilonica* (PSUC_FEM_254498). 41, *Eubothrus beheni* (USNMENT 01557990). 42. *Eubothrus leuzeae* (PSUC_FEM_253107).

the Middle East, and other regions (Nieves-Aldrey 2005, Melika 2006, Pujade-Villar and Schiopu 2015). While Buffington et al. (2020) reported that *Aylax* had been introduced to North America, there is no evidence of establishment in the Nearctic at this time, although some Aylacini are frequently intercepted at ports of entry among plant material (Buffington, pers. obs.).

Included genera.—*Aylax* Hartig, 1840 (Figs. 60; 63); *Barbotinia* Nieves-Aldrey, 1994b (Figs. 61; 64); *Iraella* Nieves-Aldrey, 1994b (Figs. 62; 65).

Remarks.—Aylacini originally included all herb-galling cynipids, but was recently restricted to a group of 7 species galling *Papaver* L. (Papaveraceae) (Ronquist et al. 2015). One species, *Fumariphilus hypecoi*

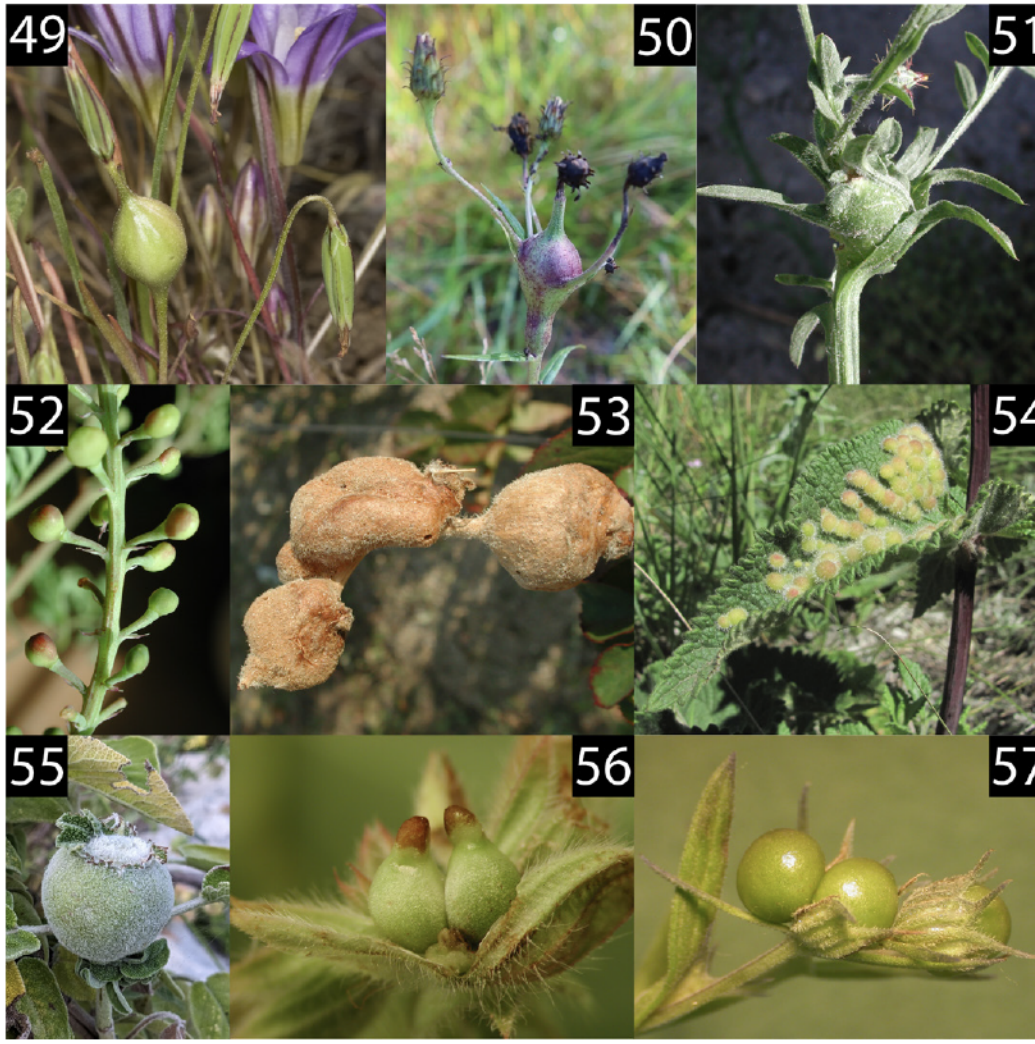
Figs. 43–48. Aulacideini adult female lateral habiti. Figure 43. *Fumariphilus versicolor* (MNCN) Figure 44. *Hedickiana levantina* (USNMENT 01790182). Figure 45. *Liposthenes glechomae* (INHS 282150). Figure 46. *Neaylax verbenacus* (PSUC_FEM_81691). Figure 47. *Panteliella fedtschenkoi* (USNMENT 01823223). Figure 48. *Rhodus cyprius* (CASENT 8526947).

(Trotter, 1913), was recently transferred from *Aylax* to *Fumariphilus* in the Aulacideini (Nieves-Aldrey 2022). After Nieves-Aldrey's revision, Aylacini is circumscribed to include only a monophyletic group of 6 species in three genera, all gall inducers on *Papaver*.

Buffington et al. (2020) reported that *Aylax* contained 20 species, while only 2 species are truly placed in the genus. This error apparently resulted from an unpublished species checklist that included species that have long been transferred elsewhere (e.g., *Aulacidea*; *Isocolus*) but were erroneously included as valid *Aylax* species.

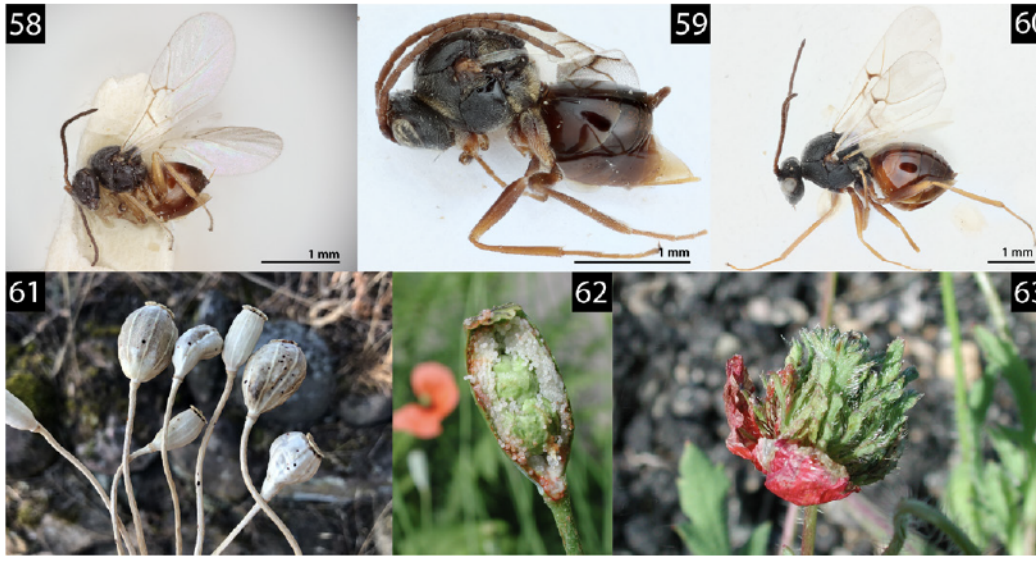
Diastrophini Nieves-Aldrey, Nylander, and Ronquist, 2015

Diagnosis.—Pronotum in dorsal view long, with medial height about 1/4 to 1/3 as long as outer lateral margins. Pronotal plate



Figs. 49–57. Galls of Aulacideini. 49, *Antistrophus microseris* (McCracken and Egbert, 1922) on *Microseris* sp., photographed by Aaron Schustef, used with permission. 50, *Aulacidea hieracii* on *Hieracium* sp., photographed by matero, licensed via CC BY-NC 4.0. 51, *Eubothrus lichtensteini* on *Centaurea* sp., photographed by José Luis Nieves-Aldrey. 52, *Fumariphilus versicolor* on *Fumaria* sp., photographed by José Luis Nieves-Aldrey. 53, *Hedickiana levantina* on *Salvia* sp., photographed by José Luis Nieves-Aldrey. 54, *Panteliella fedtschenkoi* (Rubsaamen, 1896) on *Phlomoides tuberosa*, photographed by Gennadiy Okatov, licensed via CC BY-NC 4.0. 55, *Rhodus cyprius* on *Salvia* sp., photographed by Sean Birk Bek Craig, licensed via CC BY-NC 4.0. 56, *Neaylax verbenacus* on *Salvia verbenaca*., photographed by José Luis Nieves-Aldrey. 57, *Liposthenes kerneri* on *Nepeta hispanica*., photographed by José Luis Nieves-Aldrey.

complete, with edges reaching the anterior mesoscutum and forming a conspicuously raised plate (Figs. 5–6). Pronotal submedial pits conspicuous, apparent as a pair of ovate impressions (Fig. 5–6). Tarsal claws with conspicuous basal lobes (Figs. 9–11). Antennae with 12 to 15 antennomeres in females and 13 to 15 antennomeres in males. Fore wing with or without areolet, with marginal cell entirely open, entirely closed, or



Figs. 58–63. Aylacini. F58, *Aylax minor* (INHS 288691 female lateral habitus. 59, *Barbotinia orianensis* (USNM), female lateral habitus. 60, *Iraella ionescui* (USNMENT 01231864), female lateral habitus. 61, Gall of *Aylax papaveris* on *Papaver* sp. Photographed by José Luis Nieves-Aldrey. 62, Gall of *Barbotinia orianensis* on *Papaver* sp. Photographed by José Luis Nieves-Aldrey. 63, Gall of *Iraella hispanica* on *Papaver* sp. Photographed by José Luis Nieves-Aldrey.

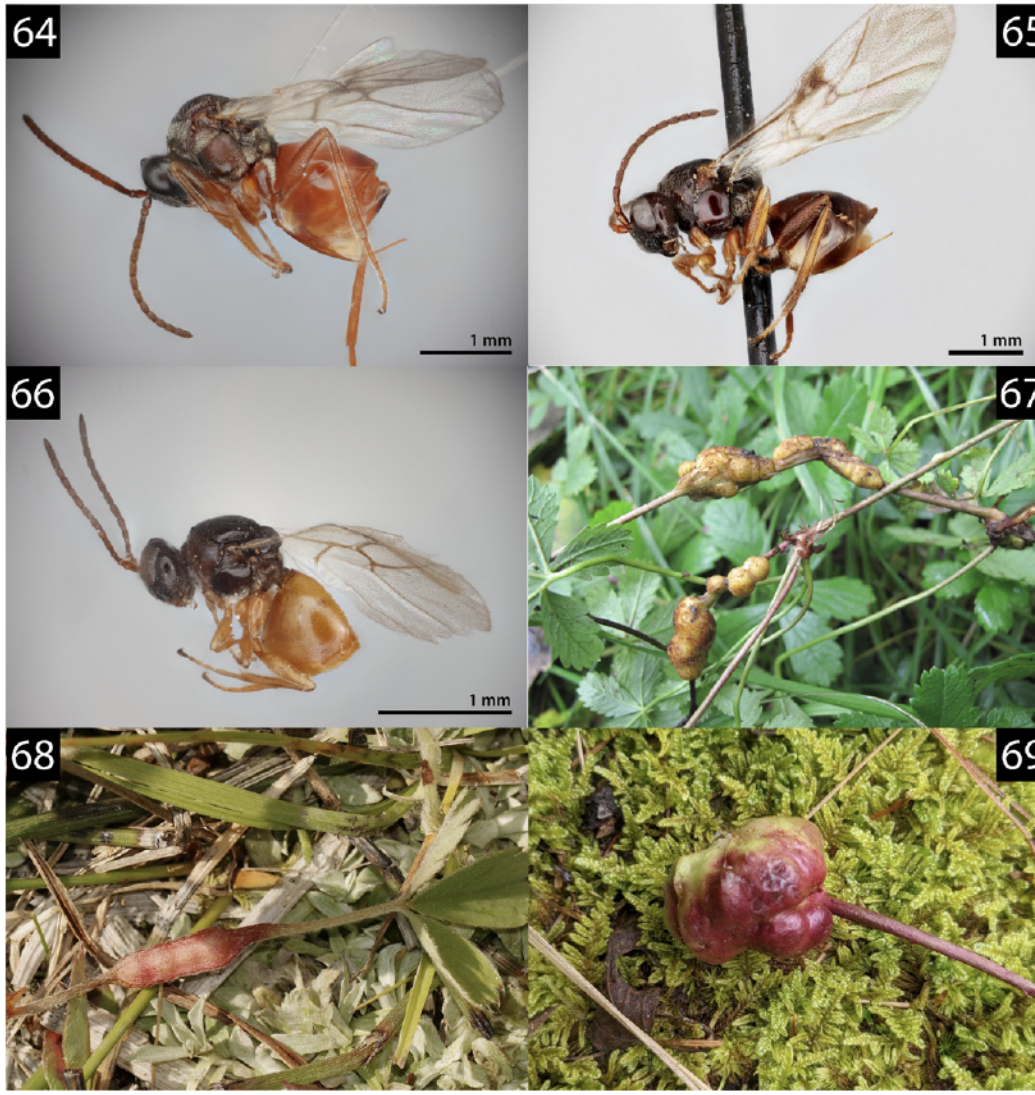
partially closed. Galls on Rosaceae, especially *Potentilla* (Figs. 69–70) and *Rubus* (Fig. 71), or inquilines in galls on Rosaceae.

Biology.— Gall inducers on Rosaceae, including both shrubby and herbaceous hosts, or inquilines in cynipid galls on Rosaceae. Known host genera for gall-inducing species are *Fragaria* L., *Potentilla* L., and *Rubus* L. Inquilinous species are associated with galls of *Diastrophus* Hartig, 1840 on *Rubus* or Diplolepidinae (Cynipoidea: Diplolepididae) on *Rosa* L. The biology of *Xestophanopsis* Pujade-Villar and Wang, 2019, is unknown; it may be an inquiline as seen in some morphologically similar taxa (Pujade-Villar et al. 2019).

Distribution.— Primarily Holarctic; most species known from North America (Nastasi and Deans 2021, Nastasi et al. 2024b), with several species known from western and central Europe, Japan (Melika 2006, Ronquist et al. 2015, Pujade-Villar et al. 2016), and Taiwan (Davis et al. 2024); a single species, *Diastrophus colombianus* Nieves-Aldrey, 2013, is known from the Neotropics (Colombia) (Nieves-Aldrey et al. 2013). Two species of *Diastrophus* are known from Taiwan (Davis et al., 2024).

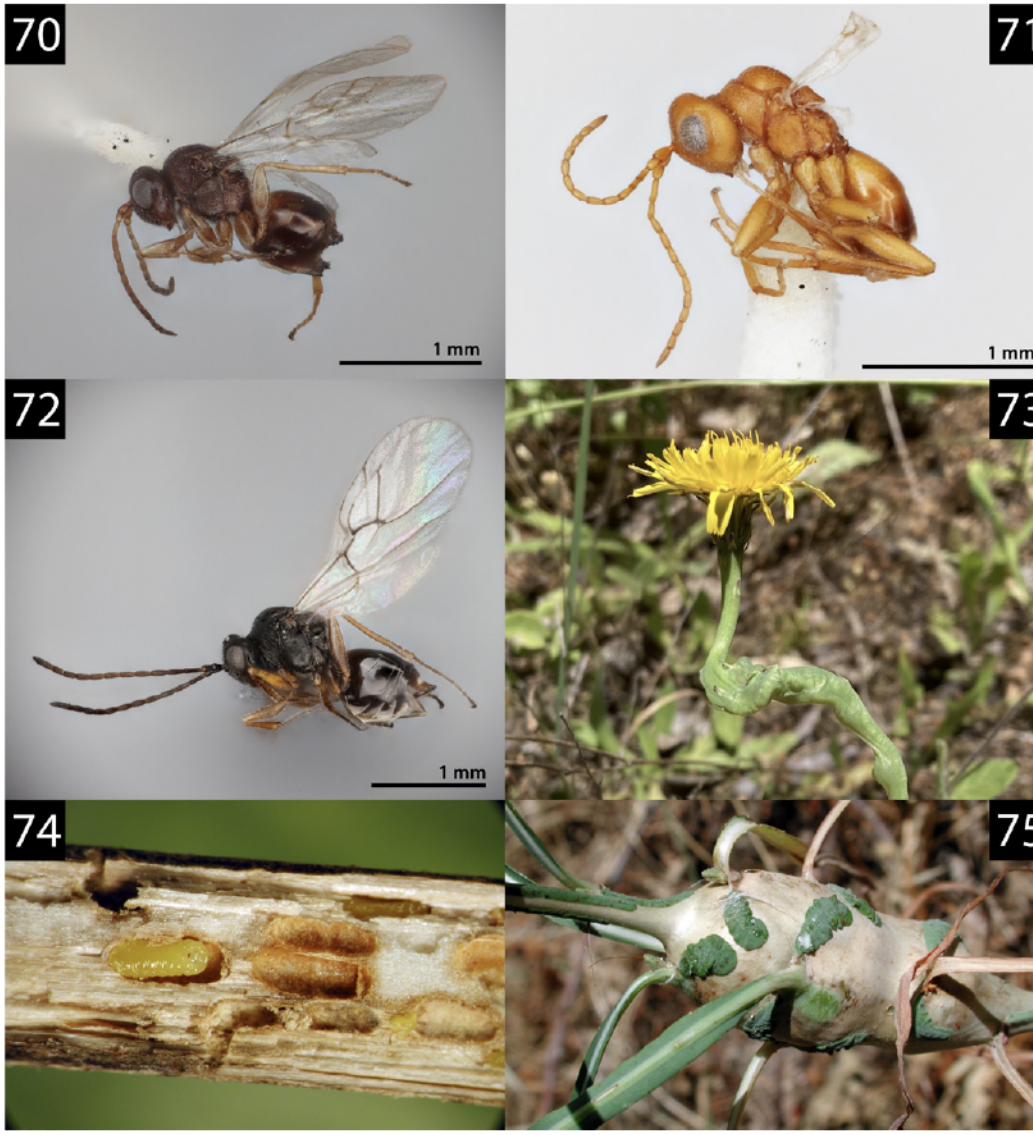
Included genera.—*Diastrophus* Hartig, 1840 (Figs. 4; 66–67; 70–71); *Periclistus* Förster, 1869; *Synophromorpha* Ashmead, 1903; *Xestophanes* Förster, 1869 (Figs. 68–69); *Xestophanopsis* Pujade-Villar and Wang, 2019.

Remarks.—Overall, Diastrophini is especially notable amongst gall wasp tribes due to the inclusion of both gall-inducing and inquilinous taxa. Two genera, *Diastrophus* and *Xestophanes*, are gall inducers on several host taxa, while two other genera, *Periclistus* and *Synophromorpha*, are inquilines of cynipid galls on *Rosa* L. and *Rubus* L. respectively. The biology of the final genus, *Xestophanopsis*, is unknown, and could represent either a gall inducer or inquiline due to morphological similarities to taxa of other life history.



Figs. 64–69. Diastrophini. Scale bars: 1.0 mm. 64, *Diastrophus potentillae* (PSUC_FEM_271945) female, lateral habitus. 65, *Diastrophus wushei* (EMUS_CYN_0021) female, lateral habitus. 66, *Xestophanes* sp. (PSUC_FEM_271915) female, lateral habitus. 67, Gall of *Xestophanes potentillae* on *Potentilla* sp., photographed by José Luis Nieves-Aldrey. 68, Gall of *Diastrophus fragariae* on *Fragaria virginiana*, photographed by Dustin Snider, used with permission. 69, Gall of *Diastrophus bassetti* on *Rubus* sp.

Diastrophus, the most species rich genus in the tribe, is capable of inducing galls on both herbaceous and woody plants. Most described *Diastrophus* species induce galls on *Rubus*; however, ongoing revisionary work suggests that species inducing galls on herbaceous plants in the Potentilleae are more diverse than those on *Rubus* (Davis et al., unpublished data). The same work suggests that complicated taxonomy of host plants has obscured true host species for several *Diastrophus*, particularly for species associated with *Rubus*. The genus *Xestophanes* is also associated with herbaceous plants, represented by several Palearctic species.



Figs. 70–75. Phanacidini. 70, *Phanacis taraxaci* (CNC_1943012) female, lateral habitus. 71, *Phanacis centaureae* (USNMENT01823221) male, lateral habitus. 72, *Phanacis hypochoeridis* (PSUC_FEM_271946) female, lateral habitus. 73, Gall of *Phanacis hypochoeridis* on *Hypochaeris radicata*, photographed by Dean Lyons, licensed via CC BY-NC 4.0. female, lateral habitus. 74, Gall of *Phanacis centaureae* on *Centaurea ornata*. Photographed by José Luis Nieves-Aldrey. 75, Gall of *Phanacis phoenixopodos* on *Lactuca viminea*. Photographed by José Luis Nieves-Aldrey.

Phanacidini Nieves-Aldrey, Nylander, and Ronquist, 2015

Diagnosis.—Pronotum in dorsal view somewhat long, with medial height usually about 1/4 as long as outer lateral margins. Pronotal plate short and incomplete, with lateral edges marked only for a short distance dorsally (Figs. 18; 23–24). Pronotal submedial pits effaced, apparent mostly as a single linear impression (Figs. 23–24). Tarsal claws

simple, without lobes (Fig. 14). Antennae with 13 or 14 antennomeres in females and 14 or 15 antennomeres in males. Fore wing with or without areolet, with marginal cell usually partly closed (Fig. 22) but rarely entirely open or closed. Galls on herbaceous plants other than Rosaceae or *Papaver* (Papaveraceae) (Figs. 1; 76–77).

Biology.—Nearly all species are gall inducers on Asteraceae; Known host genera in the Asteraceae are the following: *Carthamus* L., *Centaurea* L., *Cichorium* L., *Cirsium* Mill., *Cousinia* Cass., *Crepis* L., *Epilasia* (Bunge) Benth. and Hook., *Eryngium* L., *Hypochaeris* L., *Lactuca* L., *Lapasna* L., *Oteospermum* L., *Picris* L., *Saussurea* DC., *Serratula* L., *Silybum* L., *Sonchus* L., *Taraxacum* L., *Urospermum* Scop. Most species induce galls in stems, while species of Aulacideini induce galls on many plant organs including the stems.

In terms of host records outside of Asteraceae, one species is apparently associated with *Phlomis* L. (Lamiaceae), while two others are recorded from *Eryngium* L. and *Heracleum* L. (Apiaceae), although these records require validation. In the case of associations with Apiaceae, these are likely records on Asteraceae as some Cardueae and other composite plants resemble *Eryngium* and *Heracleum* when senesced (Nieves-Aldrey, pers. obs.).

Distribution.—Species are endemic to the Palearctic throughout Europe, temperate Asia, and parts of northern Africa, except for one described species and numerous undescribed species known from South Africa (Melika and Prinsloo 2007, van Noort et al. 2015, Nastasi et al. pers. obs.). Several species of *Phanacis* have been introduced elsewhere either accidentally or intentionally as biocontrol agents. *Phanacis hypochoeridis* (Kieffer, 1887) has been introduced to Australia, New Zealand, Chile, South Africa, and North America (Melika and Prinsloo 2007, Nieves-Aldrey and Grez 2007, Paretas-Martínez 2012, van Noort et al. 2015, Nastasi and Deans 2021). *Phanacis cichorii* has been recorded from Chile (Nieves-Aldrey and Grez 2007). *Phanacis taraxaci* (Ashmead, 1897) has also been recorded from various localities in North America (Nastasi and Deans 2021, Earley 2024).

Included genera.—*Asiocynips* Kovalev, 1982; *Diakontschukia* Melika, 2006; *Phanacis* Förster, 1860 (Figs. 72–77); *Zerovia* Diakontschuk, 1988. Some authors (e.g., Nieves-Aldrey 1994b) recognize the genus *Timaspis* Mayr, 1881, but it was synonymized by Melika (2006), which we follow here (see also remarks below).

Remarks.—Many species of Phanacidini require revision, particularly species occurring east of the Mediterranean. The genera also require revision as Ronquist et al. (2015) found that *Asiocynips* may render *Phanacis* paraphyletic, and *Diakontschukia* and *Zerovia* have not been included in recent phylogenetic analyses. *Timaspis* Mayr, 1881 has also been recognized by some authors, but phylogenetic studies (e.g., Ronquist et al. 2015) show that it may be best treated as a synonym of *Phanacis* as suggested by some others (e.g., Melika 2006), which we follow here. A comprehensive phylogenetic analysis and species-level revision of Phanacidini will be necessary to produce a more stable classification.

Checklist of World Herb-galling Cynipoidea

We do not treat the inquilinous taxa of Diastrophini in the below checklist. However, we tentatively include the genus *Xestophanopsis* Pujade-Villar and Wang, 2019 as its biology is unknown and its morphological similarity to *Xestophanes* Förster, 1869 suggests that it could be a gall inducer associated with an herbaceous species of Rosaceae (Pujade-Villar et al. 2019). We also include all described species of the genus *Diastrophus* Hartig, 1840 as there are no recent global checklists for this genus despite not all species being associated with herbaceous plants.

Aulacideini Nieves-Aldrey, Nylander, and Ronquist, 2015

(96 species in 11 genera, Nearctic and Palearctic but introduced or undescribed elsewhere)

References: Askew et al. 2006, Azmaz and Katılmış, 2020, 2021, Buffington et al. 2017, Karimpour et al. 2008, Melika 2004, 2006, Melika and Gharaei 2006, Melika and Karimpour 2012, Nastasi and Deans 2021, 2024a, 2024b, 2024c, 2024d, Nastasi et al. 2024a, 2024b, 2024c, 2024d, 2024e, in review, Nieves-Aldrey 1994a, 1994b, 1995, 2001, 2004, 2012, 2022, Pujade-Villar et al. 2014, 2016, Quinlan 1968, Quinlan and Askew 1969, Şchiopu et al. 2024, Tavakoli et al. 2022, Vyrzhikovskaya 1962, Wiśnowski and Baran 2020.

Antistrophus Walsh, 1869
(11 species, Nearctic)

Type species: *Antistrophus lygodesmiaepisum* Walsh, 1869 (=*Antistrophus pisum* [Ashmead, 1885]).

bicolor Gillette, 1891
Host plant: Presumably a species of *Silphium* L. (Asteraceae) (see Nastasi and Deans 2021; Nastasi et al. 2024c).
Distribution: Nearctic, Illinois (USA).

chrysothamni (Beutenmüller, 1908)
Host plant: Presumably a species of *Chrysothamnus* Nutt. (Asteraceae).
Distribution: Nearctic, Arizona (USA).

jeanae Tooker and Hanks, 2004
Host plant: *Silphium perfoliatum* L. (Asteraceae).
Distribution: Nearctic, Midwestern USA.

laciniatus Gillette, 1891
Host plants: *Silphium gracile* A.Gray, *S. integrifolium* Michx., *S. laciniatum* L., *S. terebinthinaceum* Jacq. (Asteraceae).
Distribution: Nearctic, Eastern and Midwestern USA.

laurenae Nastasi, 2024
Host plant: *Silphium integrifolium* Michx. (Asteraceae).
Distribution: Nearctic, Midwestern USA.

meganae Tooker and Hanks, 2004
Host plant: *Silphium terebinthinaceum* Jacq. (Asteraceae).
Distribution: Nearctic, Midwestern USA.

microseris (McCracken and Egbert, 1922)
Host plant: *Microseris* sp. (Asteraceae).
Distribution: Nearctic, California (USA).

minor Gillette, 1891
Host plant: *Silphium laciniatum* L. (Asteraceae).
Distribution: Nearctic, Midwestern USA.

pisum Walsh, 1869
Host plant: *Lygodesmia juncea* D.Don. (Asteraceae).
Distribution: Nearctic, Midwestern USA.

rufus Gillette, 1891
Host plant: *Silphium laciniatum* L. (Asteraceae).
Distribution: Nearctic, Midwestern USA.

silphii Gillette, 1891
Host plants: *Silphium integrifolium* Michx., *S. perfoliatum* L.; possibly *S. speciosum* Nutt. (see Nastasi et al. 2024c) (Asteraceae).
Distribution: Nearctic, Eastern and Midwestern USA.

Aulacidea Ashmead, 1897
(44 species, Nearctic and Palearctic)

Type species: *Aulax mulgediicola* Ashmead, 1896 (=*Aulacidea harringtoni* [Ashmead, 1887]).

abdita Kinsey, 1920
Host plant: *Lactuca canadensis* L. (Asteraceae).
Distribution: Nearctic, Massachusetts (USA).

abdominalis (Thomson, 1877)
Host plants: *Scorzonera humilis* L., *S. parviflora* Jacq., *S. purpurea* L., *S. rosea* K.K. (Asteraceae).
Distribution: Palearctic, widespread.

acroptilonica Tyurebaev, 1972
Host plant: *Leuzea repens* (L.) D.J.N. Hind (Asteraceae).

Distribution: Palearctic, Eastern Europe and Middle East; introduced to Western Nearctic for biological control.

ambrosiaecola (Ashmead, 1896)
Host plant: *Ambrosia* L. sp. (Asteraceae) (doubtful association - see Nastasi and Deans 2021).
Distribution: Nearctic, Missouri (USA).

andrei (Kieffer, 1900)
Host plant: *Hypochaeris* L. spp. (Asteraceae).
Distribution: Palearctic.

andriescui Şchiopu, Tataroğlu, and Katılmış, 2024
Host plant: *Sonchus palustris* L. (Asteraceae).
Distribution: Palearctic, Romania.

annulata Kinsey, 1920
Host plant: *Lactuca* sp. (Asteraceae).
Distribution: Nearctic, Massachusetts and Nebraska (USA).

ascanica Diakontschuk, 1984
Host plant: *Serratula xeranthemoides* M.B. (Asteraceae).
Distribution: Palearctic, Ukraine.

brevicornis Diakontschuk, 1981
Host plant: *Serratula xeranthemoides* M.B. (Asteraceae).
Distribution: Palearctic, Ukraine.

diakontschukae Melika and Klymenko, 2005
Host plant: *Phlomis tuberosa* L. (Lamiaceae).
Distribution: Palearctic, Ukraine.

discolor Diakontschuk, 1988
Host plant: *Centaurea* spp.; *Echinops* spp. (Asteraceae).
Distribution: Palearctic, Tajikistan and Turkmenistan.

follioti Barbotin, 1972
Host plant: *Sonchus asper* (L.) Hill. (Asteraceae).
Distribution: Palearctic, Western Europe. Recently found to be widespread in North America (Nastasi and Deans 2024b).

freesei Nieves-Aldrey, 1995
Host plant: *Silybum marinum* L. (Asteraceae).
Distribution: Palearctic, France.

harringtoni (Ashmead, 1887)
Host plant: *Lactuca* spp. (Asteraceae).
Distribution: Nearctic, Eastern and Midwestern.

hei Wang, Liu, and Chen, 2012
Host plant: Unknown.
Distribution: Palearctic, China and Russia.

hieracii (Linnaeus, 1758)
Host plant: *Hieracium* spp. (Asteraceae).
Distribution: Palearctic, widespread; present in Nearctic but unclear whether introduced or endemic (see Nastasi et al. 2024a).

idoneus (Belizin, 1973)
Host plant: Unknown.
Distribution: Palearctic, Israel.

irani Melika and Gharaei, 2006
Host plant: Unknown.
Distribution: Palearctic, Iran.

koeiana Melika, Tavakoli, and Stone, 2022
Host plant: *Centaurea koeiana* Bornm. (Asteraceae).
Distribution: Palearctic, Iran.

koelpiniae Diakontschuk, 1988
Host plant: *Koelpinia linearis* Pall. (Asteraceae).
Distribution: Palearctic, Turkmenistan.

laurae Nieves-Aldrey, 1992
Host plant: *Scorzonera laciniata* L. (Asteraceae).
Distribution: Palearctic, Spain.

lorestanica Melika, Tavakoli, and Stone, 2022
Host plant: *Centaurea pterocaula* Trautv. (Asteraceae).
Distribution: Palearctic, Iran.

manchuria Nastasi, 2024
Host plant: Unknown, presumably a Hieraciinae (Asteraceae) (see Nastasi and Deans 2024a).
Distribution: Palearctic, China.

martae Nieves-Aldrey, 2004
Host plant: *Launaea arborescens* (Batt.) Murb.
Distribution: Palearctic, Spain.

nabali (Brodie, 1892)
Host plant: *Nabalus* spp. (Asteraceae).
Distribution: Nearctic, Eastern USA and Canada.

nibletti Quinlan and Askew, 1969
Host plant: *Hieracium vulgatum* Fr. (Asteraceae).
Distribution: Palearctic, Scotland.

parvula Diakontschuk, 1984
Host plants: *Echinops* spp.; *Cousinia* spp.; *Centaurea* spp. (Asteraceae); *Eryngium* spp. (Apiaceae; probable misidentification).
Distribution: Palearctic, Tajikistan and Turkmenistan.

phlomica Belizin, 1959
Host plant: *Phlomis tuberosa* L. (Lamiaceae).
Distribution: Palearctic, Russia and Ukraine.

pilarae Nieves-Aldrey, 2012
Host plant: *Serratula nudicaulis* (L.) DC. (Asteraceae).
Distribution: Palearctic, Spain.

pilosellae (Kieffer, 1901)
Host plant: *Pilosella* spp. (Asteraceae).
Distribution: Palearctic, widespread; apparently introduced to USA.

piroziae Melika, Stone, and Pujade-Villar, 2022
Host plant: *Centaurea pterocaula* Trautv. (Asteraceae).
Distribution: Palearctic, Iran.

podagrae (Bassett, 1890)
Host plant: *Lactuca* spp. (Asteraceae).
Distribution: Nearctic, Eastern and Midwestern USA.

pumila (Giraud, 1859)
Host plant: Unknown.
Distribution: Palearctic.

rubi Diakontschuk, 2003
Host plant: *Rubus idaeus* L. (Rosaceae; dubious record).
Distribution: Palearctic, Ukraine.
Comments: Unlikely to be a true valid species; likely a rearing error and subsequent misidentification (Nieves-Aldrey, pers. obs.).

scorzonerae (Giraud, 1859)
Host plant: *Scorzonera austriaca* Willd. (Asteraceae).
Distribution: Palearctic, Eastern Europe.

serratulae Diakontschuk, 1984
Host plant: *Serratula bracteifolia* (Iljin) Stank., *S. coronata* L., *S. tianshanica* L. (Asteraceae)
Distribution: Palearctic, Eastern Europe and Middle East.

subterminalis Niblett, 1946
Host plant: *Pilosella* spp. (Asteraceae).
Distribution: Palearctic, widespread; introduced to USA, Canada, New Zealand; possibly elsewhere.

taurica (Belizin, 1954)
Host plant: Unknown.
Distribution: Palearctic, Ukraine.

tavakolii Melika, 2008
Host plant: *Tragopogon marginatus* Pavlov, *T. porrifolius* L. (Asteraceae).
Distribution: Palearctic, Middle East.

tobiasi Melika, 2004
Host plant: *Saussurea grandifolia* Max., *S. pulchella* (Fischer) DC. (Asteraceae).
Distribution: Palearctic, Russia.

tragopogonis (Thomson, 1877)
Host plants: *Tragopogon dubius* Scop., *T. majus* Jacq., *T. orientalis* L., *T. porrifolius* L., *T. pratense* L. (Asteraceae).
Distribution: Palearctic, widespread.

tumida (Bassett, 1890)
Host plant: *Lactuca canadensis* L. (Asteraceae).
Distribution: Nearctic, Eastern USA.

turcica Azmaz and Katılmış, 2020
Host plant: *Digitalis ferruginea* (Plantaginaceae; probably erroneous - see Nastasi and Deans 2024a)
Distribution: Palearctic, Türkiye.
turguti Azmaz and Katılmış, 2021
Host plant: *Hieracium patentissimum* Freyn and Sint. (Asteraceae).
Distribution: Palearctic, Türkiye.

Cecconia Kieffer, 1902
(1 species, Palearctic)

Type species: *Aulax valerianellae* (Thomson, 1877) (=*Cecconia valerianellae* [Thomson, 1877]).
valerianellae (Thomson, 1877)
Host plants: *Valeriana carinata* Loisel, *V. dentata* Pöllich, *V. locusta* L., *V. olitoria* (L.) Mönch, *V. rimosa* Bast. (Caprifoliaceae).
Distribution: Palearctic, widespread.

Eubothrus Förster, 1869
(=*Isocolus* Förster, 1869; 25 species, Palearctic)

Type species: *Diastrophus scabiosae* Giraud, 1859 (=*Isocolus scabiosae* [Giraud, 1859]).
barakus (Nastasi, 2024) **comb. nov.**
Host plant: Unknown.
Distribution: Palearctic, Kyrgyzstan.
beheni (Melika and Karimpour, 2008) **comb. nov.**
Host plants: *Centaurea ammoyanus* (L.), *C. behen* L., *C. bruguierana* (DC.) Hand. (Asteraceae).
Distribution: Palearctic, Iran.
belizini (Diakontschuk, 1981) **comb. nov.**
Host plants: *Chartolepis intermedia* Boiss. (Asteraceae).
Distribution: Palearctic, Kazakhstan.
brunneus (Diakontschuk, 1982) **comb. nov.**
Host plants: *Inula hirta* L. (Asteraceae).
Distribution: Palearctic, Ukraine.
carthami (Diakontschuk, 2003) **comb. nov.**
Host plants: *Carthamus lanatus* L. (Asteraceae).
Distribution: Palearctic, Ukraine.
centaureae (Diakontschuk, 1982) **comb. nov.**
Host plants: *Centaurea diffusa* Lam., *C. pseudomaculosa* Dobrocz., *C. squarrosa* (Boiss.), *C. stoebe* L. (Asteraceae).
Distribution: Widespread in Western and Central Palearctic.
cirsii (Diakontschuk, 1987) **comb. nov.**
Host plants: *Cirsium ukrainicum* Bess. (Asteraceae).
Distribution: Palearctic, Ukraine.
cousiniae (Diakontschuk, 1988) **comb. nov.**
Host plants: *Cousinia bipinnata* Boiss. (Asteraceae).
Distribution: Palearctic, Turkmenistan.
fitchi (Kieffer, 1898) **comb. nov.**
Host plants: *Centaurea scabiosa* L. (Asteraceae).
Distribution: Palearctic, Europe.
flavus (Diakontschuk, 1982) **comb. nov.**
Host plants: *Centaurea orientalis* L. (Asteraceae).
Distribution: Palearctic, Ukraine.
freidbergi (Melika, 2008) **comb. nov.**
Host plants: *Centaurea verutum* L. (Asteraceae).
Distribution: Palearctic, Israel.
jaceae (Schenck, 1863) **comb. nov.**
Host plants: *Centaurea glastifolia* L., *C. jacea* L., *C. montana* L., *C. paniculata* L., *C. rhenana* Bor., *C. scabiosa* L. (Asteraceae).
Distribution: Palearctic, Europe.
karimpouri (Melika and Tavakoli, 2008) **comb. nov.**
Host plants: *Klasea cerinthifolia* (Sm.) Boiss. (Asteraceae).
Distribution: Palearctic, Iran.
lichtensteini (Mayr, 1882) **comb. nov.**
Host plants: *Centaurea aspera* L., *C. melitensis* L., *C. salmantica* L. (Asteraceae).
Distribution: Palearctic, Western Europe.
leuzeae (Nieves-Aldrey and Parra, 2003) **comb. nov.**
Host plants: *Leuzea conifera* (L.). (Asteraceae).
Distribution: Palearctic, Spain.

melikai (Pujade-Villar, 2014) **comb. nov.**
Host plants: *Centaurea ornata* Willd. (Asteraceae).
Distribution: Palearctic, Spain.
phaeopappucii (Diakontschuk, 1983) **comb. nov.**
Host plants: *Centaurea trinervius* (Steph.) Boiss. (Asteraceae).
Distribution: Palearctic, Ukraine.
ponticus (Diakontschuk, 1982) **comb. nov.**
Host plants: *Centaurea adpressa* Ledeb., *C. solstitialis* L. (Asteraceae).
Distribution: Palearctic, Ukraine.
rogenhoferi (Wachtl, 1880) **comb. nov.**
Host plants: *Centaurea* spp. (Asteraceae).
Distribution: Palearctic, Europe.
ruthenicae (Diakontschuk, 1983) **comb. nov.**
Host plants: *Centaurea ruthenica* Lam. (Asteraceae).
Distribution: Palearctic, Russia and Ukraine.
scabiosae (Giraud, 1859) **comb. rev.**
Host plants: *Centaurea* spp. (Asteraceae).
Distribution: Palearctic, Europe.
serratulae (Mayr, 1882) **comb. nov.**
Host plants: *Serratula bracteifolia* (Iljin) Stank., *S. heterophylla* Desf., *S. radiata* (Waldst. and Kit.), *S. xeranthemoides* M.B. (Asteraceae).
Distribution: Palearctic, Europe.
similis (Diakontschuk, 1982) **comb. nov.**
Host plants: *Centaurea breviceps* Iljin. (Asteraceae).
Distribution: Palearctic, Ukraine.
tinctorius (Melika and Gharaei, 2006) **comb. nov.**
Host plants: *Carthamus tinctorius* L. (Asteraceae).
Distribution: Palearctic, China, Iran, Iraq.
volgensis (Diakontschuk, 1982) **comb. nov.**
Host plants: *Centaurea adpressa* Ledeb. (Asteraceae).
Distribution: Palearctic, Russia and Ukraine.

Fumariphilus Nieves-Aldrey, 2022
(2 species, Palearctic)

Type species: *Aylax versicolor* Nieves-Aldrey, 1985 (=*Fumariphilus versicolor* [Nieves-Aldrey, 1985]).
hypecoi (Trotter, 1913)
Host plants: *Hypecoum imberbe* A, *H. procumbeus* A. (Papaveraceae).
Distribution: Palearctic, widespread.
versicolor (Nieves-Aldrey, 1985)
Host plants: *Fumaria capreolata* A., *officinalis* A. (Papaveraceae).
Distribution: Palearctic, Western Europe.

Hedickiana Nieves-Aldrey, 1994b
(1 species, Palearctic)

Type species: *Aulacidea levantina* Hedicke, 1928 (=*Hedickiana levantina* [Hedicke, 1928]).
levantina (Hedicke, 1928)
Host plants: Recorded from species of *Salvia* L. and *Phlomis* L. (Lamiaceae), but only records on *Salvia* (*S. pomifera* L., *S. syriaca* L., *S. triloba* L.) appear accurate.
Distribution: Palearctic, primarily Eastern Europe and Middle East.

Liposthenes Förster, 1869
(3 species, Nearctic and Palearctic)

Type species: *Aulax glechomae* Hartig, 1841 (=*Liposthenes glechomae* [Linnaeus, 1758]; basionym *Cynips glechomae* Linnaeus, 1758).
glechomae (Linnaeus, 1758)
Host plant: *Glechoma hederacea* L. (Lamiaceae).
Distribution: Palearctic, widespread; introduced to eastern Nearctic.
hymenocrateris Diakontschuk, 1983
Host plant: *Nepeta bituminosa* Fisch. and C.A.Mey (Lamiaceae).
Distribution: Palearctic, Turkmenistan.
kerneri (Wachtl, 1891)
Host plants: *Nepeta cataria* L., *N. grandiflora* Bieb., *N. hispanica* Boiss.

and Reuter, *N. latifolia* DC., *N. nuda* L., *N. parviflora* M.B., *N. ucrainica* (Lamiaceae).
Distribution: Palearctic, widespread.

Neaylax Nieves-Aldrey, 1994b
(4 species, Palearctic but recently recorded from Nearctic)

Type species: *Aulax salviae* Giraud, 1859 (=*Neaylax salviae* [Giraud, 1859]).
nemorosae (Balás, 1940)
Host plant: *Salvia nemorosa* L. (Lamiaceae).
Distribution: Palearctic.
salviae (Giraud, 1859)
Host plants: *Salvia nemorosa* L., *S. nutans* L., *S. officinalis* L., *S. pratensis* L., *S. sclarea* L., *S. silvestris* L., *S. transsilvanica* L. (Lamiaceae).
Distribution: Palearctic, widespread.
verbenacus (Nieves-Aldrey, 1988)
Host plant: *Salvia pratensis* L., *S. verbenaca* L. (Lamiaceae).
Distribution: Palearctic, Western Europe; recently reported in Manitoba, Canada (Nastasi et al. 2024a).
verticillica (Belizin, 1959)
Host plant: *Salvia verticillata* L. (Lamiaceae).
Distribution: Palearctic, Russia.

Panteliella Kieffer, 1901
(3 species, Palearctic)

Type species: *Aulax fedtschenkoi* Rübsaamen, 1896 (=*Panteliella fedtschenkoi* [Rübsaamen, 1896]).
bianchii Vyrzhikovskaya, 1962
Host plant: Unknown.
Distribution: Palearctic, Russia.
fedtschenkoi (Rübsaamen, 1896)
Host plant: *Phlomis tuberosa* (L.) Moench. (Lamiaceae).
Distribution: Palearctic, Eastern Europe and Mongolia.
rugosa Nastasi, 2024
Host plant: Unknown.
Distribution: Palearctic, Kyrgyzstan.

Rhodus Quinlan, 1968
(1 species, Palearctic)

Type species: *Diastrophus cyprius* Houard, 1919 (=*Rhodus cyprius* [Houard, 1919]).
cyprius (Houard, 1919)
Host plants: Recorded from species of *Salvia* L. and *Phlomis* L. (Lamiaceae), but only records on *Salvia* spp. appear accurate.
Distribution: Palearctic, Mediterranean and Middle East.

Soparia Nastasi, 2024 *in* Nastasi and Deans, 2024c
(1 species, Palearctic)

Type species: *Soparia oshensis* Nastasi, 2024
oshensis Nastasi, 2024 *in* Nastasi and Deans, 2024e.
Host plant: Unknown.
Distribution: Palearctic, Kyrgyzstan.

Aulacideini nomina dubia
(see taxonomic treatment of Aulacideini)

Aulacidea arnicae Hoffmeyer, 1930
Host plant: *Arnica montana* L. (Asteraceae).
Distribution: Palearctic, Denmark.

Aylacini Ashmead, 1903
(6 species in 3 genera, Palearctic)

References: Nieves-Aldrey 1994b, 2001, 2005, Melika 2006, Pujade-Villar and Schiopu 2015.

Aylax Hartig, 1840
(2 species, Palearctic)

Type species: *Cynips rhoeadis* Bouché, 1834 (=*Aylax papaveris* [Perris, 1840]).
minor Hartig, 1840
Host plants: *Papaver argemone* L., *P. dubium* L., *P. hybridum* L., *P. rhoeas* L. (Papaveraceae).

Distribution: Palearctic, widespread.

papaveris (Perris, 1840)

Host plants: *Papaver dubium* L., *P. rhoeas* L., *P. somniferum* L. (Papaveraceae).

Distribution: Palearctic, widespread.

Barbotinia Nieves-Aldrey, 1994b
(1 species, Palearctic)

Type species: *Aylax oraniensis* Barbotin, 1964 (=*Barbotinia oraniensis* [Barbotin, 1964]).

oraniensis (Barbotin, 1964)

Host plants: *Papaver dubium* L., *P. hybridum* L., *P. rhoeas* L. (Papaveraceae).

Distribution: Palearctic, widespread.

Iraella Nieves-Aldrey, 1994b
(3 species, Palearctic)

Type species: *Aulax luteipes* Thomson, 1877 (=*Iraella luteipes* [Thomson, 1877]).

hispanica Nieves-Aldrey, 2005

Host plant: *Papaver somniferum* L. (Papaveraceae).

Distribution: Palearctic, Spain.

ionescui Pujade-Villar and Schiopu, 2015

Host plant: *Papaver dubium* L., *P. rhoeas* L. (Papaveraceae).

Distribution: Palearctic, Romania.

luteipes (Thomson, 1877)

Host plants: *Papaver bracteatum* Lindl., *P. pseudorientale* L., *P. somniferum* L. (Papaveraceae).

Distribution: Palearctic, widespread.

Diastrophini Nieves-Aldrey, Nylander, and Ronquist, 2015
(includes 25 gall-inducing species in 3 genera; inquilines not treated here)

References: Nieves-Aldrey 2001, Nieves-Aldrey et al. 2013, Liu 2004, Melika 2006, Wachi et al. 2013, Pujade-Villar et al. 2019, Gates et al. 2020, Nastasi and Deans 2021, Davis et al. 2024.

Diastrophus Hartig, 1840
(21 species, Nearctic, Neotropical, Palearctic)

Type species: *Cynips rubi* (Bouché, 1834) (=*Diastrophus rubi* [Bouché, 1834]).

austrior Kinsey, 1922

Host plant: *Rubus parviflorus* Nutt. (Rosaceae).

Distribution: Nearctic, California (USA).

bassettii Beutenmüller, 1892

Host plants: *Rubus flagellaris* Willd., *R. hispidus* L. (Rosaceae).

Distribution: Nearctic, widespread in eastern USA.

colombianus Nieves-Aldrey, 2013

Host plant: *Rubus glaucus* Bent. (Rosaceae).

Distribution: Neotropical, Colombia.

cuscutaeformis Osten Sacken, 1863

Host plant: *Rubus* spp. (Rosaceae).

Distribution: Nearctic, Eastern USA and southern Canada.

fragariae Beutenmüller, 1915

Host plant: *Fragaria virginiana* Duch. (Rosaceae).

Distribution: Nearctic, Northeastern USA and southern Canada.

fusiformans Ashmead, 1890

Host plant: *Potentilla* sp. (Rosaceae).

Distribution: Nearctic, Western USA.

hieracii Melika and Klymenko, 2005

Host plant: Erroneously recorded from *Hieracium* sp. (Asteraceae).

Distribution: Palearctic, Ukraine.

japonicus Wachi, Ide, and Abe, 2013

Host plant: *Rubus palmatus* Thunb. (Rosaceae).

Distribution: Palearctic, Japan.

kincaidii Gillette, 1893

Host plant: *Rubus parviflorus* Nutt. (Rosaceae).

Distribution: Nearctic, with disjunct populations in the Great Lakes region and in the Pacific Northwest.

mayri Reinhard, 1876
Host plants: *Potentilla argentea* L., *P. canescens* Bess., *P. heptaphylla* L., *P. impolita* Wahlenb., *P. subpoena* L., *P. wiemanniana* Günth. and Schum. (Rosaceae).
Distribution: Palearctic, widespread in Europe and possibly parts of Asia.

nebulosus (Osten Sacken, 1861)
Host plant: *Rubus* spp. (Rosaceae).
Distribution: Nearctic, widespread in Eastern USA and southern Canada.

niger Bassett, 1900
Host plant: *Potentilla canadensis* L. (Rosaceae).
Distribution: Nearctic, widespread in Eastern USA and southern Canada.

piceus Provancher, 1886
Host plant: Unknown.
Distribution: Nearctic, Ontario (Canada).

potentillae Bassett, 1864
Host plants: *Potentilla canadensis* L., *P. simplex* Michx. (Rosaceae).
Distribution: Nearctic, widespread in United States and southern Canada.

radicum Bassett, 1870
Host plants: *Rubus flagellaris* Willd., *R. occidentalis* L. (Rosaceae).
Distribution: Nearctic, widespread in Eastern United States.

renai Davis and Nastasi, 2024
Host plant: Unknown.
Distribution: Palearctic, Taiwan.

rubi (Bouché, 1834)
Host plants: *Rubus caesius* L., *R. fruticosus* L., *R. hirtus* L., *R. idaeus* L., *R. seebergensis* Pfuhl., *R. ulmifolius* Schott (Rosaceae).
Distribution: Palearctic, widespread throughout Europe.

smilacis Ashmead, 1896
Host plant: Unknown; formerly believed to induce galls on *Smilax* but probably truly associated with *Rubus* (Gates et al. 2020).
Distribution: Nearctic, Illinois (USA).

tumefactus Kinsey, 1920
Host plant: *Potentilla norvegica* L. (Rosaceae).
Distribution: Nearctic, Southern Canada and Northeastern USA.

turgidus Bassett, 1870
Host plant: *Rubus strigosus* Michx. (Rosaceae).
Distribution: Nearctic, widespread in northern USA and Canada.

wushei Davis and Nastasi, 2024
Host plant: Unknown.
Distribution: Palearctic, Taiwan.

Xestophanes Förster, 1869
(3 species, Palearctic)

Type species: *Cynips potentillae* Retzius, 1783 (=*Xestophanes potentillae* [Retzius, 1783]).

brevitarsis (Thomson, 1877)
Host plants: Usually *Potentilla erecta* L.; other records include *P. arenaria* Borkh., *P. canescens* Bess, *P. heptaphylla* L., *P. verna* L. (Rosaceae).
Distribution: Palearctic, Western Europe.

caspiana Liu, 2004
Host plant: Unknown.
Distribution: Palearctic, Azerbaijan.

potentillae (Retzius, 1783)
Host plants: Usually *Potentilla reptans* L.; other records include *P. argentea* L., *P. arenaria* Borkh., *P. canescens* Bess, *P. erecta* L., *P. heptaphylla* L., *P. impolita* Wahlenb., *P. pimpinelloides* L., *P. silesiaca* Uechtr., *P. sterilis* (L.) Garcke. (Rosaceae).
Distribution: Palearctic, widespread throughout Europe.

Xestophanopsis Pujade-Villar and Wang, 2019
(1 species, Palearctic)

Type species: *Ceroptres distinctus* Wang, Liu, and Chen, 2012 (=*Xestophanopsis distinctus* [Wang, Liu, and Chen, 2012]).

distinctus (Wang, Liu, and Chen, 2012)
Host plant: Unknown (biology unclear; other Diastrophini are gall inducers or inquilines).
Distribution: Palearctic, China.

Phanacidini Nieves-Aldrey, Nylander, and Ronquist, 2015
(Palearctic but widely introduced elsewhere, 41 species in 4 genera)

References: Kovalev 1982, Diakontschuk 1988, Nieves-Aldrey 1994a, 1994b, 1995, 2008, Nieves-Aldrey et al. 2008, Melika 2006, Melika and Prinsloo 2007, Azmaz and Katılmış, 2021, Tavakoli and Melika 2006, Tavakoli et al. 2022.

Asiocynips Kovalev, 1982
(4 species, Palearctic)

Type species: *Asiocynips pannucea* Kovalev, 1982.

caulina Diakontschuk, 1988
Host plant: *Cousinia bipinnata* Boiss. (Asteraceae).
Distribution: Palearctic, Tajikistan and Turkmenistan.

cousiniae Diakontschuk, 1988
Host plants: *Cousinia refracta* Jur. (Asteraceae).
Distribution: Palearctic, Tajikistan.

lugubris Kovalev, 1982
Host plant: *Cousinia* sp. (Asteraceae).
Distribution: Palearctic, Kazakhstan.

pannucea Kovalev, 1982
Host plant: *Cousinia* sp. (Asteraceae).
Distribution: Palearctic, Tajikistan and Uzbekistan.

Diakontschukia Melika, 2006
(1 species, Palearctic)

Type species: *Phanacis saussureae* Diakontschuk, 2001 (=*Diakontschukia saussureae* [Diakontschuk, 2001]).

saussureae (Diakontschuk, 2001)
Host plants: *Saussurea neopulchella* Lipsch., *S. pulchella* (Fisch.) (Asteraceae).
Distribution: Palearctic, Russia.

Phanacis Förster, 1860
(35 species, Palearctic with 1 endemic Afrotropical species; widely introduced elsewhere)

Type species: *Phanacis centaureae* Förster, 1860.

carthami Gussakovkij, 1933
Host plant: *Carthamus* sp. (Asteraceae).
Distribution: Palearctic, Ukraine and Uzbekistan.

caulicola (Hedicke, 1939)
Host plants: *Picris echioides* L., *O. hieracioides* L. (Asteraceae).
Distribution: Palearctic, widespread in Europe.

centaureae Förster, 1860
Host plants: *Centaurea aspera* L., *C. diffusa* Zam., *C. jacea* L., *C. micranthos* Gmel., *C. nigra* L., *C. pseudomaculosa* Dobrocz., *C. rhenana* Boreau, *C. scabiosa* L., *C. stenolepis* A.Kern., *C. solstitialis* L., *C. squarrosa* (Boiss.) (Asteraceae).
Distribution: Palearctic, widespread in Europe.

chondrillae (Gain, 1894)
Host plant: *Chondrilla juncea* L. (Asteraceae).
Distribution: Palearctic, Europe.

ciceki Azmaz and Katılmış, 2021
Host plant: *Picris* sp. (Asteraceae).
Distribution: Palearctic, Türkiye.

cichorii (Kieffer, 1909)
Host plant: *Cichorium intybus* L. (Asteraceae).
Distribution: Palearctic, widespread in Europe but also known from Asia

including South Caucasus and Turkmenistan.

comosae Nieves-Aldrey, 2008
Host plant: *Picris comosa* Benth. (Asteraceae).
Distribution: Palearctic, Spain.

cousiniae Diakontschuk, 1988
Host plants: *Centaurea* spp., *Cousinia* spp. (Asteraceae).
Distribution: Palearctic, Tajikistan and Turkmenistan.

crassinervis Diakontschuk, 1980
Host plants: *Centaurea* spp. (Asteraceae).
Distribution: Palearctic, Ukraine.

dobrogicus Şchiopu, Tataroğlu, and Katılmış, 2024
Host plant: *Crepis foetida rhoeadifolia* (M. Bieb.) Čelak (Asteraceae).
Distribution: Palearctic, Romania.

eryngi (Diakontschuk, 1984)
Host plant: *Eryngium* sp. (Apiaceae; host record highly suspect).
Distribution: Palearctic, Georgia.

eugeniae (Diakontschuk, 1981)
Host plant: *Serratula* sp. (Asteraceae).
Distribution: Palearctic, Ukraine.

helmintheae (De Stefanii, 1902)
Host plant: *Helminthotheca aculeata* (Vahl) Lack (=*Helminthia aculeata*; *Picrisaculeata*) (Asteraceae).
Distribution: Palearctic, Italy.

heraclei (Hedicke, 1923)
Host plant: *Heracleum sphondylum* L. (Apiaceae; host record highly suspect)
Distribution: Palearctic, Germany.

heteropappi Diakontschuk, 1988
Host plant: *Centaurea canescens* L. (Asteraceae).
Distribution: Palearctic, Turkmenistan.

hypochoeridis (Kieffer, 1887)
Host plants: *Hypochaeris glabra* L., *H. radicata* L. (Asteraceae).
Distribution: Palearctic, Europe and Northern Africa; widely introduced elsewhere (see treatment of Phanacidini above).

irani (Tavakoli and Melika, 2006)
Host plant: *Lactuca orientalis* Boiss. (Asteraceae).
Distribution: Palearctic, Iran.

kiefferi (Cotte, 1915)
Host plant: *Carthamus lanatus* L. (Asteraceae).
Distribution: Palearctic, France and Spain.

lampsanae (Perris, 1873)
Host plant: *Lapsana communis* L. (Asteraceae).
Distribution: Palearctic, widespread in Europe.

lorestanicus (Tavakoli and Melika, 2006)
Host plant: *Lactuca orientalis* Boiss. (Asteraceae).
Distribution: Palearctic, Iran.

lusitanica (Tavares 1903)
Host plant: *Crepis vesicaria* L. (Asteraceae).
Distribution: Palearctic, widespread in Europe.

maculatus Diakontschuk, 1988
Host plant: *Centaurea squarrosa* (Boiss.) (Asteraceae).
Distribution: Palearctic, Tajikistan.

neserorum Melika and Prinsloo, 2007
Host plant: *Osteospermum moniliferum* L. (Asteraceae).
Distribution: Afrotropical, South Africa.

phlomidis Belizin, 1959
Host plant: *Phlomis tuberosa* L. (Lamiaceae).
Distribution: Palearctic, Russia and Ukraine.

phoenixopodos (Mayr, 1882)
Host plants: *Lactuca saligna* L., *L. viminea* (L.) J.Presl. (Asteraceae).
Distribution: Palearctic, widespread in Europe and Northern Africa.

pilicornis (Thomson, 1877)
Host plant: Unknown.
Distribution: Palearctic, Sweden.

rufipes Ionescu and Roman, 1959
Host plant: *Crepis pulchra* L. (Asteraceae).
Distribution: Palearctic, Romania.

sonchi (De Stefani, 1900)
Host plant: *Sonchus asper* L. (Asteraceae).
Distribution: Palearctic, Mediterranean Europe.

strigosa Melika, Stone, and Tavakoli, 2022
Host plant: *Picris strigosa* M.Bieb. (Asteraceae).
Distribution: Palearctic, Iran.

taraxaci (Ashmead, 1897)
Host plant: *Taraxacum officinale* L. (Asteraceae).
Distribution: Palearctic, widespread in Europe; introduced elsewhere (see treatment of Phanacidini above).

tavakolii Melika, Stone, and Pujade-Villar, 2022
Host plant: *Cichorium intybus* L. (Asteraceae).
Distribution: Palearctic, Iran.

urhani Azmaz and Katılmış, 2021
Host plant: *Cirsium vulgare* (Savi) Ten.
Distribution: Palearctuc, Türkiye.

urospermi (Kieffer, 1901)
Host plant: *Urospermum picroides* (L.) (Asteraceae).
Distribution: Palearctic; Spain, Portugal, and Northern Africa.

varians Diakontschuk, 1980
Host plants: *Centaurea adpressa* L., *C. orientalis* L. (Asteraceae).
Distribution: Palearctic, Ukraine.

zwoelferi Nieves-Aldrey, 1995
Host plant: *Silybum marinum* L. (Asteraceae).
Distribution: Palearctic, widespread in Europe.

Zerovia Diakontschuk, 1988
(1 species, Palearctic)

Type species: *Zerovia asiaemediae* Diakontschuk, 1988.

asiaemediae Diakontschuk, 1988
Host plant: *Epilasia* sp. (Asteraceae).
Distribution: Palearctic, Turkmenistan.

Discussion

Studies in recent decades have greatly elucidated our understanding of herb gall wasps across all tribes. Perhaps the most important result is confirmation of molecular tools being useful for species delimitation in herb gall wasps. Our recent findings in the Nearctic suggest that DNA barcoding using the *cytochrome c oxidase subunit I* fragment can be effective for delimiting species of herb gall wasps (e.g., Nastasi et al. 2024d). Applying molecular markers to the Palearctic fauna will likely allow for elucidation of many species concepts, and should be prioritized for species that are currently understood to be highly polyphagous, especially those of interest in biological control (Nastasi and Deans 2024a).

More generally, recent studies have suggested that herb gall wasps are far more diverse than previously understood, especially in regions where they have not been abundantly studied in recent years (e.g., Nastasi et al. 2024d). Similarly, our knowledge of herb gall wasps in tropical regions is beginning to improve, as several species are known from the Southern Hemisphere, with additional undescribed species known to the authors (see above taxonomic treatments).

Numerous herb gall wasps have been examined as biological control agents for their host plants. Several species of *Aulacidea* have been used to control hawkweeds and knapweeds in North America and elsewhere (Nastasi and Deans 2021, Nastasi and Deans 2024a and references therein, Nastasi and Davis 2022). Additional species, especially *Aulacidea* and *Phanacis*, have been mentioned as possible agents but have apparently not been seriously considered (Nieves-Aldrey et al. 2004, Nieves-Aldrey 2008, Mason 2021, Cripps 2024). Given that many species of herb gall wasps are evidently capable of inhibiting host plant reproduction, either by altering flower and/or seed development (e.g., *Antistrophus silphii* Gillette [1891] as

reported by Fay and Hartnett [1991]) or by attacking structures used in vegetative spread (e.g., *Aulacidea subterminalis* Niblett, 1946 as reported by Klöppel et al. [2003]), more species could be evaluated as desirable control agents. Such potential is further suggested by the broad overlap in gall wasp host plants and plants known to be invasive in North America alone (Swearingen and Bargeron 2016).

Lastly, the independent use of the same host plants in Aulacideini and Phanacidini, especially taxa in the Cardueae and Cichorieae (Asteraceae), also warrants further study. Species of *Aulacidea* and *Eubothrus* (Aulacideini) share many of the same host plants used by Phanacidini; many such "species pairs" also induce similar galls, are sympatric, and have overlapping phenologies (Ronquist and Liljeblad 2001, Nieves-Aldrey et al. 2004, Melika 2006). While the reasons for this pattern are currently unclear, some studies indicate that this convergence could be the product of ancestral interspecific parasitism or inquilinism as seen in other Cynipoidea (Ronquist and Liljeblad 2001, Nieves-Aldrey et al. 2004, Nieves-Aldrey 2012).

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Literature Cited

Askew, R. R., Plantard, O., Gómez, J. F., Hernández-Nieves, M. and Nieves-Aldrey, J. L. 2006. Catalogue of parasitoids and inquilines in galls of Aylacini, Diplolepidini and Pediaspidini (Hym., Cynipidae) in the West Palaearctic. Zootaxa 1301: 1–60.

Azmaz, M. and Katılmış, Y. 2020. A new species of herb gall wasp (Cynipidae, Aulacideini, *Aulacidea*) from Turkey. Zootaxa 4747: 378–390. https://doi.org/10.11646/zootaxa.4747.2.9.

Azmaz, M. and Katilmış, Y. 2021. Three new species of herb gall wasps (Hymenoptera: Cynipidae) from Turkey. European Journal of Taxonomy 757: 152–168. https://doi.org/10.5852/ejt.2021.757.1421.

Buffington, M. L., Forshage, M., Liljeblad, J., Tang, C. T. and van Noort, S. 2020. World Cynipoidea (Hymenoptera): a key to higher-level groups. Insect Systematics and Diversity 4(4): 1. https://doi.org/10.1093/isd/ixaa003.

Buffington, M. L., Prasifka, J. R., Gates, M. W., Kula, R. R. and Peterson, K. 2017. New host plant and distribution records for *Antistrophus laciniatus* Gillette, 1891 (Hymenoptera: Cynipidae), an herb gall wasp on *Silphium integrifolium* Michx. (Asteraceae), with notes on other *S. integrifolium*-associated wasps. Proceedings of the Entomological Society of Washington 119(4): 660–666. https://doi.org/10.4289/0013-8797.119.4.660.

Cripps, M. 2024. Potential for biocontrol of *Silybum marianum* (variegated thistle): 2. Literature search and prioritisation of biocontrol agents. New Zealand Entomologist 47: 20–34. https://doi.org/10.1080/00779962.2024.2309001.

Davis, C. K., Nastasi, L. F., and Deans, A. R. 2024. Description of two new species of Diastrophus Hartig, 1840 from Taiwan, *Diastrophus renai* and *D. wushei*. Zootaxa 5541(3): 367–374. https://doi.org/10.11646/zootaxa.5541.3.7.

Deans, A. R., Nastasi, L. F., and Davis, C. K. 2024. GallOnt: An ontology for plant gall phenotypes. Biodiversity Data Journal.

Biodiversity Data Journal 12: e128585. https://doi.org/10.3897/BDJ.12.e128585.

Diakontschuk, L. A. 1988. New and little known cynipids of the subfamily Cynipinae (Hymenoptera, Cynipidae) from middle Asia. Entomologicheskoe Obozrenie 67: 166–181.

Early, N. G. 2024. First record in British Columbia for the dandelion gall wasp, *Phanacis taraxaci* (Ashmead) (Hymenoptera: Cynipidae, Phanacidini). Specimen 31. https://doi.org/10.56222/28166531.2024.31.

Fay, P. A. and Hartnett, D. C. 1991. Constraints on growth and allocation patterns of *Silphium integrifolium* (Asteraceae) caused by a cynipid gall wasp. Oecologia 88: 243–250.

Förster, A. 1869. Ueber die Gallwespen. Verhandlungen der Kaiserlich-Königlichen Zoologisch-botanischen Gesellschaft in Wien 19: 325–370.

Gates, M. W., Zhang, Y. M. and Buffington, M. L. 2020. The great greenbriers gall mystery resolved? New species of *Aprostocetus* Westwood (Hymenoptera, Eulophidae) gall inducer and two new parasitoids (Hymenoptera, Eurytomidae) associated with *Smilax* L. in southern Florida, USA. Journal of Hymenoptera Research 80: 71–98. https://doi.org/10.3897/jhr.80.59466.

Goulet, H. and Huber, J. T. 1993. Hymenoptera of the World: An Identification Guide to Families. Agriculture Canada, Ottawa, Ontario. 680 pp.

International Commission on Zoological Nomenclature. 1999. International Code Of Zoological Nomenclature. The International Trust for Zoological Nomenclature 1999.

Karimpour, Y., Tavakoli, M. and Melika, G. 2008. New species of herb gallwasps from the Middle East (Hymenoptera, Cynipidae, Aylacini). Zootaxa 1854(1): 16–32. https://doi.org/10.11646/zootaxa.1854.1.2.

Klöppel, M., Smith, L., and Syrett, P. 2003. Predicting the impact of the biocontrol agent Aulacidea subterminalis (Cynipidae) on growth of Hieracium pilosella (Asteraceae) under differing environmental conditions in New Zealand. Biocontrol Science and Technology 13(2): 207–218.

Kovalev, O. V. 1982. Cynipid gall-makers of the subfamily Aylacinae (stat. n.)(Hym., Cynipidae) and their species described within the family Figitidae. Trudy Zoologicheskogo Instituta Akademiji Nauk SSSR 110: 85–93.

Liu, Z. 2004. A new species of *Xestophanes* Förster (Hymenoptera: Cynipidae) from Azerbaijan. Proceedings of the Entomological Society of Washington, 106(4): 779–783.

Mason, P. G. (ed.) 2021. Biological Control: Global Impacts, Challenges and Future Directions of Pest Management. CRC Publishing, Boca Raton, Florida, USA. 644 pp.

Melika, G. 2004. A new species of gall wasp from the Russian Far East (Hymenoptera: Cynipidae, Aylacini). Proceedings of the Russian Entomological Society, St. Petersburg, 75(1): 214–218.

Melika, G. 2006. Gall wasps of Ukraine, Volume 1. Vestnik zoologii, The Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine. 300 pp.

Melika, G. and Gharaei, B. 2006. New species of herb galling cynipids (Hymenoptera: Cynipidae: Aylacini) from Iran. Acta Zoological Academiae Scientiarum Hungaricae 52(4): 385–399.

Melika, G. and Karimpour, Y. 2012. Herb gallwasp fauna of Iran (Hymenoptera: Cynipidae, Aylacini). North-western Journal of Zoology 8(2): 268–277.

Melika, G. and Prinsloo, G. L. 2007. *Phanacis neserorum* sp. n. (Hymenoptera: Cynipidae: Aylacini): first record of a phytophagus Afrotropical cynipoid gall wasp. African Entomology 15(1): 185–191. https://doi.org/10.4001/1021-3589-15.1.185.

Nastasi, L. F., Ammann, R. and Deans, A. R. 2024a. Discovery of the Palearctic species *Neaylax verbenacus* (Nieves-Aldrey, 1988) (Hymenoptera: Cynipidae: Aulacideini) in Manitoba, Canada. Specimen 33. https://doi.org/10.56222/28166531.2024.33.

Nastasi, L. F., Buffington, M. L., Davis, C. K. and Deans, A. R. 2024b. Key to the North American tribes and genera of herb, rose, bramble, and inquiline gall wasps (Hymenoptera, Cynipoidea, Cynipidae sensu lato). ZooKeys 1196: 177–207. https://doi.org/10.3897/zookeys.1196.118460.

Nastasi, L. F. and Davis, C. K. 2022. Field guide to the herb and bramble gall wasps of North America. Frost Entomological Museum, The Pennsylvania State University, University Park, Pennsylvania, USA. https://doi.org/10.26207/rn61-fk81.

Nastasi, L. F. and Deans, A. R. 2021. Catalogue of Rose Gall, Herb Gall, and Inquiline Gall Wasps (Hymenoptera: Cynipidae) of the United States, Canada and Mexico. Biodiversity Data Journal 9. https://doi.org/10.3897/BDJ.9.e68558.

Nastasi, L. F. and Deans, A. R. 2024a. *Aulacidea manchuria* Nastasi sp. nov., a new herb gall wasp from China (Hymenoptera: Cynipoidea:

Aulacideini), with commentary on hawkweed gall wasps (Asteraceae: Hieraciinae). Zootaxa 5492(4): 582–588. https://doi.org/10.11646/zootaxa.5492.4.6.

Nastasi, L. F. and Deans, A. R. 2024b. Discovery of *Aulacidea follioti* Barbotin, 1972 (Hymenoptera: Cynipidae: Aulacideini) in the United States and Canada. Journal of the Entomological Society of Ontario 155.

Nastasi, L. F. and Deans, A. R. 2024c. New herb gall wasps (Hymenoptera: Cynipidae: Aulacideini) from Kyrgyzstan, with description of a new genus and a review of the genus *Panteliella* Kieffer, 1901. Zootaxa 5537(4): 511–526. https://doi.org/10.11646/zootaxa.5537.4.4.

Nastasi, L. F. and Deans, A. R. 2024d. New country record and commentary for *Aulacidea hei* Wang et al. (Hymenoptera: Cynipidae: Aulacideini). Specimen 36. https://doi.org/10.56222/28166531.2024.36.

Nastasi, L. F., Davis, C. K., Alcorn, J. K., Frey, T. S., Hatfield, M. J., Hines, H. M., Tooker, J. F. and Deans, A. R. 2024c. Two new *Ormyrus* Westwood (Chalcidoidea: Ormyridae) from cynipid galls on *Silphium* L. (Asteraceae: Heliantheae). Zootaxa 5601: 265-287.

Nastasi, L. F., Smith, C. N., Tooker, J. F. and Deans, A. R. 2024d. Catalog of endophytic insects associated with rosinweeds (*Silphium* L., Heliantheae, Asteraceae) in North America. Psyche: a Journal of Entomology 8464635. https://doi.org/10.1155/2024/8464635.

Nastasi, L. F., Tooker, J. F., Davis, C. K., Smith, C. N., Frey, T. S., Hatfield, M. J., Presnall, T. M., Hines, H. M. and Deans, A. R. 2024e. Cryptic or underworked? Taxonomic revision of the *Antistrophus rufus* species complex (Cynipoidea, Aulacideini). Journal of Hymenoptera Research 97: 399–439. https://doi.org/10.3897/jhr.97.121918.

Nieves-Aldrey, J. L. 1994a. Revision of C. G. Thomson's nominal species of Aylacini (Hymenoptera: Cynipidae). Entomological Scandinavica 25: 151–158.

Nieves-Aldrey, J. L. 1994b. Revision of West-European Genera of the Tribe Aylacini Ashmead (Hymenoptera, Cynipidae). Journal of Hymenoptera Research 3: 175–206.

Nieves-Aldrey, J. L. 1995. Two New Species of Aylacini (Hymenoptera: Cynipidae) from France, Associated with *Silybum* and A New Gall from *Scorzonera* (Asteraceae). Annales de la Société entomologique de France 31(4): 396–375. https://doi.org/10.1080/21686351.1995.12277735.

Nieves-Aldrey, J. L. 2001. Hymenoptera, Cynipidae. In: Fauna Iberica Vol. 16. Ramos, M. A. et al. (Eds.). Museo Nacional de Ciencias Naturales Consejo Superior de Investigaciones Científicas. Madrid, Spain. 636 pp.

Nieves-Aldrey, J. L. 2004. A New *Aulacidea* Species (Hymenoptera, Cynipidae) From Cabo de Gata Nature Park (Spain) Inducing Galls on *Launaea arborescens*, Including Description of its Terminal Instar Larva. Graellsia 60(2): 175–184.

Nieves-Aldrey, J. L., Gómez, J. F. and Hernández Nieves, M. 2004. Nuevos datos sobre *Aulacidea freesei* y *Phanacis zwoelferi* (Hymenoptera, Cynipidae, Aylacini), inductores de agallas en *Silybum marinum* (Asteraceae), en la Península itérica, incluyendo la descripción y comparación de sus larvas terminales y sus agallas. Boletín Sociedad Entomológica Aragonesa 34: 85–93.

Nieves-Aldrey, J. L. 2005. A New Species of *Iraella* Nieves-Aldrey (Hymenoptera: Cynipidae), from Northeastern Spain, Inducing Galls on *Papaver* (Papaveraceae). Annals of the Entomological Society of America 98(6): 853–860. https://doi.org/10.1603/0013-8746(2005)098[0853:ANSOIN]2.0.CO;2.

Nieves-Aldrey, J. L. and Grez, A. 2007. Two cynipid species inducing galls to herbaceous weeds (Hym., Cynipidae) introduced in Chile. Agrociencia 41(8): 921–927.

Nieves-Aldrey, J. L. 2008. Rediscovery of *Aulacidea kiefferi* Cotte, 1915 (Hymenoptera, Cynipidae), with redescription of the adult and terminal larva. Graellsia 64(2): 295–305.

Nieves-Aldrey, J. L. 2012. Two new herb gall wasps from Spain, including the description of a new species of *Aulacidea* Ashmead, 1897 (Hymenoptera, Cynipidae, "Aylacini") inducing galls on *Serratula nudicaulis*. Graellsia 68(2): 325–339.

Nieves-Aldrey, J. L. 2022. Description of *Fumariphilus* Nieves-Aldrey, gen. nov., a new genus of herb gall wasps, with a key to genera of the tribe Aulacideini (Hymenoptera: Cynipidae). Zootaxa 5155: 393–413. https://doi.org/10.11646/zootaxa.5155.3.5.

Nieves-Aldrey, J. L., Rodríguez, P. A. and Medianero, E. 2013. Description of a New Species of *Diastrophus* (Hymenoptera: Cynipidae: "Aylacini") from Colombia: The First Herb Gall Wasp Native to the Neotropical Region. Annals of the Entomological Society of America 106(6): 719–728. https://doi.org/10.1603/AN13033.

Nieves-Aldrey, J. L., Sánchez, I., Massa, B. and Gómez, J. F. 2008. Cynipid wasps that induce galls on plants of the genus *Picris* (Asteraceae) in Europe, with a description of a new species of *Phanacis* Foerster (Hymenoptera, Cynipidae) from the Iberian Peninsula. Annales de la Société Entomologique de France 44(3): 257–269.

Paretas-Martínez, J., Forshage, M., Buffington, M., Fisher, N., La Salle, J. and Pujade-Villar, J. (2012) Overview of Australian Cynipoidea (Hymenoptera). Australian Journal of Entomology 52(1): 73–86. https://doi.org/10.1111/j.1440-6055.2012.00877.x.

PATO Curators. 2023. Phenotype and Trait Ontology. Available from https://github.com/pato-ontology/pato/. [Accessed 9 October 2024].

Penev, L., Sharkey, M., Erwin, T., van Noort, S., Buffington, M., Seltmann, K., Johnson, N., Taylor, M., Thompson, F. and Dallwitz, M. 2009. Data publication and dissemination of interactive keys under the open access model. ZooKeys 21: 1–17. https://doi.org/10.3897/zookeys.21.274.

Pujade-Villar, J. and Schiopu, I. 2015. Species of Aylacini Ashmead, 1903 (Hymenoptera: Cynipidae) inducing galls on Papaver L. (Papaveraceae) from Romania with description of a new species and notes on parasitoids (Hymenoptera). Zoosystema 37(3): 505–515. https://doi.org/10.5252/z2015n3a5.

Pujade-Villar, J., Tormos, J., González-Núñez, P. S. and Cobo, A. 2014. First report of bivoltinism in *Isocolus* (Hymenoptera, Cynipidae): *Isocolus melikai* Pujade-Villar n. sp. from the Iberian Peninsula. Zoosystema 36(1): 41–52. https://doi.org/10.5252/z2014n1a3.

Pujade-Villar, J., Wang, Y., Guo, R. and Chen, X. 2016. Revision on Palearctic species of *Periclistus* Förster with description of a new species and its host plant gall (Hymenoptera, Cynipidae). ZooKeys 596: 65–75. https://doi.org/10.3897%2Fzookeys.596.5945.

Pujade-Villar, J., Wang, Y., Liu, Z., Chen, X., He, J. and Ferrer-Suay, M. 2019. Discovery of *Xestophanopsis* gen. n. from China and taxonomic revision of two species misplaced in *Ceroptres* Hartig, 1840 (Hymenoptera, Cynipoidea: Cynipidae). Entomologica Fennica 30(3): 126–137. https://doi.org/10.33338/ef.84149.

Quinlan, J. 1968. Cynipinae (Hymenoptera) occurring on *Phlomis* L. Transactions of the Royal Entomological Society of London 120(13): 275–286.

Quinlan, J. and Askew, R. R. 1969. A new species of gall-wasp (Hymenoptera: Cynipidae) from Scotland. Proceedings of the Royal Entomological Society of London 38(1–2): 1–4.

Ronquist, F. and Liljeblad, J. 2001. Evolution of the gall wasp-host plant association. Evolution 55(12): 2503–2522. https://doi.org/10.1111/j.0014-3820.2001.tb00765.x.

Ronquist, F., Nieves-Aldrey, J. L., Buffington, M. L., Liu, Z., Liljeblad, J. and Nylander, J. A. 2015. Phylogeny, evolution and classification of gall wasps: the plot thickens. PLoS One 10(5): e0123301. https://doi.org/10.1371/journal.pone.0123301.

Şchiopu, I., Tataroğlu, M. and Katılmış, Y. 2024. New species of gall wasps (Hymenoptera: Cynipidae: Aulacideini and Phanacidini) inducing galls on plants of the genera *Sonchus* and *Crepis* (Asteraceae) in Romania (Dobrogea Province) and notes on their parasitoids. Zootaxa 5471(1): 33–55. https://doi.org/10.11646/zootaxa.5471.1.2.

Swearingen, J. and Bargeron, J. C. 2016. Invasive Plant Atlas of the United States. University of Georgia Center for Invasive Species and Ecosystem Health. Accessed 4 June 2024. Accessible at https://www.invasiveplantatlas.org/.

Tavakoli, M. & Melika, G. 2006. Two new species of *Timaspis* Mayr, 1881 from Iran (Hymenoptera: Cynipidae, Aylacini). Folia Entomologica Hungarica, 67: 207–219.

Tavakoli, M., Stone, G. N., Pujade-Villar, J. and Melika, G. 2022. New herb gall wasps from Iran (Hymenoptera: Cynipidae). Zootaxa 5155(3): 301–333. https://doi.org/10.11646/zootaxa.5155.3.1.

Tooker, J.F., Deans, A.R., and Hanks, L.M. 2004. Description of the Antistrophus rufus (Hymenoptera: Cynipidae) Species Complex, Including Two New Species. Journal of Hymenoptera Research 13: 125–133.

van Noort, S. 2024. Waspweb https://www.waspweb.org [Accessed 2024/10/18].

van Noort, S., Buffington, M. L. and Forshage, M. 2015. Afrotropical Cynipoidea (Hymenoptera). ZooKeys 493: 1–176. https://doi.org/10.3897%2Fzookeys.493.6353.

Vyrzhikovskaya, A. V. 1962. Gall-wasps (Hymenoptera, Cynipoidea, Cynipinae) of the Leningrad Region. Proceedings of the Zoological Institute of the USSR Academy of Sciences XXXI: 138–171.

Wachi, N., Ide, T. and Abe, Y. 2013. Eastern Palearctic Occurrence of *Diastrophus* (Hymenoptera: Cynipidae: Aylacini) on *Rubus* Bushes, with Description of a New Species. Annals of the Entomological Society of America 106(3): 288–293. https://doi.org/10.1603/AN12114.

Ward, D. F. 2014. Overview and key to the New Zealand Cynipoidea (Hymenoptera). Zootaxa 3878(6): 563–579.

Wiśniowski, B. and Baran, J. 2020. Trzy gatunki galasówek (Hymenoptera: Cynipidae) nowe dla fauny Polski. Acta Entomological Silesiana 28(17): 1–5. http://doi.org/10.5281/zenodo.3820034.

Yoder, M. J., Mikó, I., Seltmann, K. C., Bertone, M. A. and Deans, A. R. 2010. A gross anatomy ontology for Hymenoptera. PloS One 5(12): e15991. https://doi.org/10.1371/journal.pone.0015991.

Supplemental File 1. Lucid Interchange Format version 3 (LIF3) of the WaspWeb online Lucid matrix identification key to Cynipidae tribes (Cynipoidea, Hymenoptera). doi:10.26207/s8dt-f586

The LIF3 file is an XML-based file that stores all the Lucid3 key data, allowing exchange of the key with other key developers.