

New herb gall wasps (Hymenoptera: Cynipidae: Aulacideini) from Kyrgyzstan, with description of a new genus and a review of the genus *Panteliella* Kieffer, 1901

LOUIS F. NASTASI^{1,2} & ANDREW R. DEANS^{1,3}

¹*Frost Entomological Museum, Department of Entomology, The Pennsylvania State University, University Park, PA, 16802.*

²✉ lfnastasi@gmail.com,  <https://orcid.org/0000-0001-7825-480X>

³✉ ard19@psu.edu,  <https://orcid.org/0000-0002-2119-4663>

Abstract

We describe three new aulacideine herb gall wasp species (Hymenoptera: Cynipidae: Aulacideini) from Kyrgyzstan, a country from which only two Aulacideini species were previously known. One of our new species represents a new genus, which we describe here as *Soparia oshensis* Nastasi **gen. and sp. nov.** We describe *Panteliella rugosa* Nastasi **sp. nov.**, representing a new genus record for Kyrgyzstan. To further facilitate species recognition in *Panteliella*, we redescribe the genus and the species *P. fedtschenkoi*; provide a translated description of *P. bianchii* Vyrzhikovskaya, 1962; comment on complications affecting this genus; and provide a key to *Panteliella* species. Lastly, we describe *Isocolus barakus* Nastasi **sp. nov.**, a species with morphology atypical of *Isocolus*. We provide a key to the Kyrgyz genera of Aulacideini to ensure that they remain diagnosable for future study. Our findings illustrate the continued unveiling of a diverse herb cynipid fauna in Central Asia and a need for further taxonomic study in the region.

Key words: Aulacideini, new genus, new species, *Panteliella*, *Soparia*

Introduction

Herb gall wasps (Hymenoptera: Cynipidae: Aulacideini) comprise a diverse lineage of gall-inducing insects that use several families of herbaceous plants as hosts (Buffington *et al.* 2020, Nieves-Aldrey 2022). While the herb gall wasp diversity of the Western Palearctic has been treated by numerous studies, only two species of Aulacideini are known from Kyrgyzstan: *Aulacidea acropitilonica* Tyurebaev, 1972 (Melika 2006, Zerova *et al.* 1988, Kovalev & Diakontschuk 1986), and *Aulacidea serratulae* Diakontschuk, 1984 (Melika 2006). In the present study, we add new records for the Kyrgyz fauna based on three Aulacideini specimens collected in Kyrgyzstan and deposited at the Illinois Natural History Survey (INHS, University of Illinois, Champaign, Illinois, USA). These specimens represent a new genus as well as undescribed species in the genera *Isocolus* Förster, 1869 and *Panteliella* Kieffer, 1901.

In the case of *Panteliella*, the genus has been subject to numerous taxonomic acts and treatments, few of which agree on crucial diagnostic characters at the generic or species levels. To resolve some of these issues, we review the generic taxonomy and species of *Panteliella* and justify the establishment of the species *Panteliella rugosa* Nastasi **sp. nov.**

While the three new species are each known from only a single female specimen, none of which have associated host data, the establishment of these new species is warranted based on very limited knowledge of herb gall wasps in Kyrgyzstan, a paucity of available gall wasp material from the region, and clear morphological distinction from known species. By describing these new species, we aim to enrich knowledge of herb gall wasps in Central Asia, bring awareness to the existence of an intriguing fauna in the region that warrants further study, and expand known morphological and geographic trends in Aulacideini as a whole.

Materials and methods

Morphological terminology primarily follows the Hymenoptera Anatomy Ontology (Yoder *et al.* 2010) and the Phenotype and Trait Ontology (PATO Curators 2023). We selected morphological characters for Aulacideini from recent works on herb gall wasps, especially Melika (2006), Nieves-Aldrey (2022), and Nastasi *et al.* (2024b). Terms relating to gall phenotypes and structure were drawn from Deans *et al.* (2023, 2024). We examined specimens using an Olympus SZX16 stereo microscope (Olympus Life Science, Tokyo, Japan) fitted with an optical micrometer. We used an incandescent gooseneck illuminator fitted with mylar strips and LED light rings to produce optimal lighting conditions, especially regarding cuticular sculpture. We imaged specimens to illustrate our manuscript using a Macroscopic Solutions ‘microkit’ (Tolland, Connecticut, USA). We stacked images using Zerene Stacker LLC (Richland, Washington, USA), and edited images using Adobe Photoshop and/or Adobe Illustrator (San Jose, California, USA). We examined specimens deposited in the following collections:

- **INHS:** Illinois Natural History Survey, University of Illinois, Champaign, Illinois, USA
- **USNM:** National Museum of Natural History, Washington, DC, USA

Results

Soparia Nastasi gen. nov.

urn:lsid:zoobank.org:act:8B51576B-67DD-4194-8828-30CAC5996F15

(Figs. 1–6)

Type species: *Soparia oshensis* Nastasi sp. nov., described below.

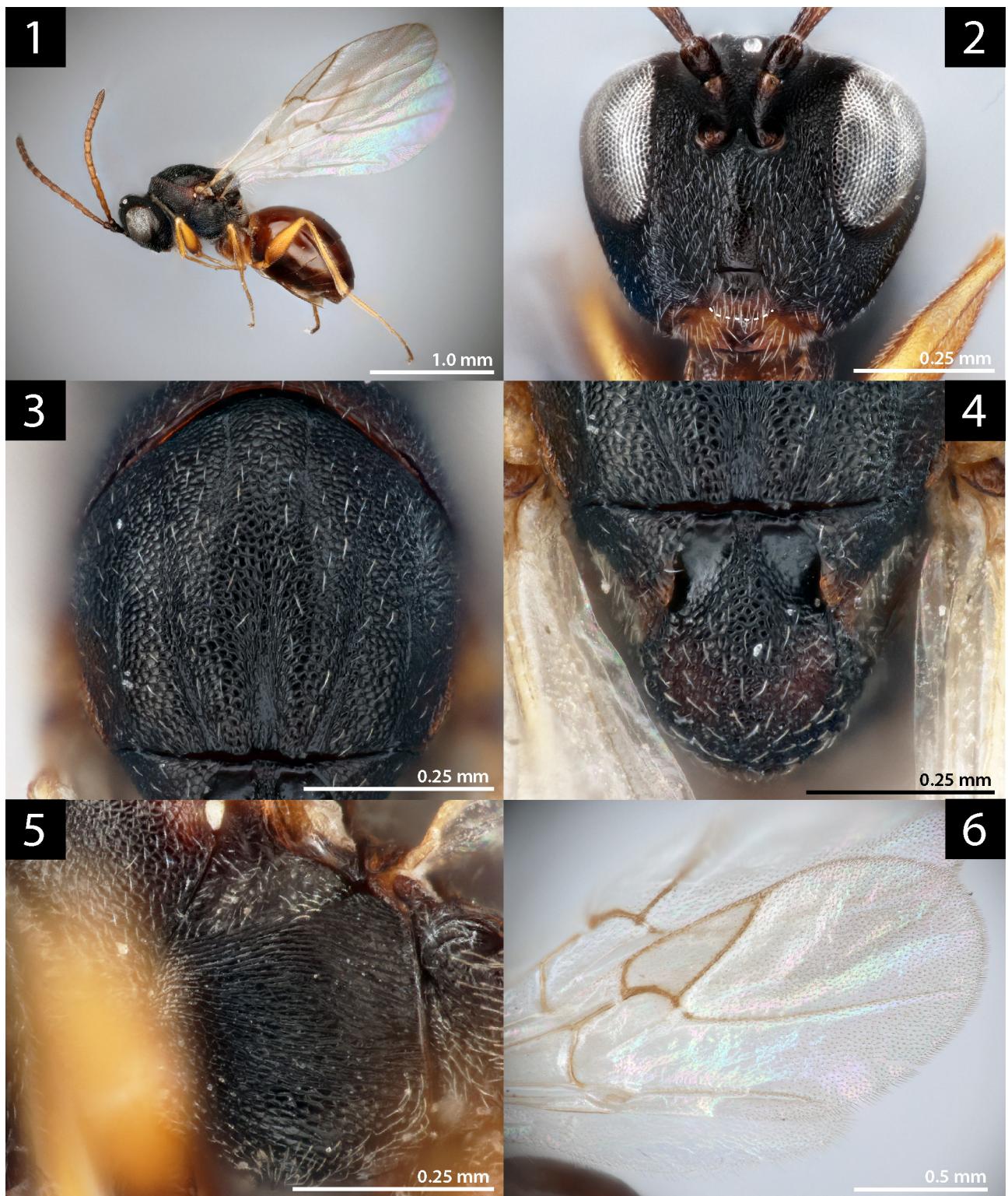
Etymology. From the Kyrgyz terms чөп and сары аары (phoneticized as *çöp* and *sari aari*), meaning “herb” and “wasp” respectively. Gender feminine, following Article 30.2.4 (International Commission on Zoological Nomenclature 1999).

Diagnosis. *Soparia* gen. nov. is distinguishable from all other genera of Aulacideini by the following combination of characters: Female antennae (Fig. 1) with 13 antennomeres, with F2 conspicuously longer than F1. Facial radiating striae conspicuous and complete, traceable from clypeus to ventral eye margin (Fig. 2). Fore wing with marginal cell closed, with areolet present but with venation faint, and with conspicuous setae along distal margin (Fig. 6). Notauli (Fig. 3) incomplete, narrow, and poorly impressed, most apparent in posterior half of mesoscutum. Mesopleuron striate-reticulate throughout (Fig. 5). Second metasomal tergite with a conspicuous anterolateral setose patch (Fig. 1).

The aforementioned characters make *Soparia* relatively similar to *Aulacidea* Ashmead, 1897, especially regarding the closed marginal cell of the fore wing and the presence of a conspicuous setose patch on the second metasomal tergite. *Soparia* is easily distinguished from *Aulacidea* by the sculpture of the mesopleuron. In *Aulacidea*, the mesopleuron is entirely striate except for several species (including *A. acroptilonica* which has been reported in Kyrgyzstan) in which there is a small area of reticulate sculpture in the ventral third. In *Soparia*, the mesopleuron is entirely striate-reticulate throughout. Similarly, *Aulacidea* species have complete, deeply impressed notauli, except for a few species in which they are weakly impressed in the anterior third. In *Soparia*, the notauli are incomplete and relatively weakly impressed throughout and are most conspicuous only in the posterior half of the mesoscutum.

Lastly, *Soparia* greatly resembles some species of the Nearctic genus *Antistrophus* Walsh, 1869. While species of *Antistrophus* exhibit striate-reticulate sculpture on the mesopleuron, they all lack a conspicuous setose patch on second metasomal tergite, and all have an open marginal cell (Nastasi *et al.* 2024a, 2024b). *Antistrophus* is also exclusively Nearctic in distribution and induces galls only on plants native to the region (Nastasi & Deans 2021, Nastasi *et al.* 2024b).

Remarks. See treatment of *Soparia oshensis* Nastasi sp. nov. below for description, biology, distribution, and remarks.



FIGURES 1–6. *Soparia oshensis* Nastasi gen. and sp. nov. All images show holotype female INHS Insect Collection 288148. (1) Lateral habitus. (2) Head in anterior view; dotted line indicates ventral margin of clypeus. (3) Mesoscutum in dorsal view. (4) Scutellum in dorsal view. (5) Mesopleuron in lateral view. (6) Wings.

***Soparia oshensis* Nastasi sp. nov.**

urn:lsid:zoobank.org:act:426D77D5-6402-4639-BD3A-9D3A4A8EA675

(Figs. 1–6)

Material examined. Holotype female: INHS Insect Collection 288148. Kyrgyzstan: Osh Region, Chon-Byuleolyu Ravine, 40°10'25" N, 73°37'23" E (approximately 40.174, 73.623 in decimal degrees). 2050m elevation. Collected 7 July 2000, by vacuum. Field code 00-087-01. C. H. Dietrich coll.

Etymology. The specific epithet refers to the type locality in the Osh Region of Kyrgyzstan. Noun in apposition.

Description of female (Fig. 1). Body 2.0 mm in length. Coloration of head and mesosoma more or less entirely black; metasoma reddish brown. Mandibles reddish brown. Antennae reddish brown, with scape and pedicel much darker than following antennomeres. Wings hyaline; veins brown. Legs yellow except coxae and femora brown proximally to yellow distally and apical tarsomeres brown.

Head (Fig. 2). In dorsal view 1.8× as wide as long; in anterior view slightly subtrapezoidal, 1.2× as wide as tall. Sculpture excluding facial radiating striae coriaceous to reticulate throughout. POL:LOL:OOL:DLO in holotype measuring 12:6:9:4. Toruli situated about mid-height of eyes. Malar space about 0.5× as long as compound eye in anterior view. Facial radiating striae complete, conspicuously impressed and reaching from clypeus to ventral eye margin. Clypeus large, trapezoidal, and moderately projecting ventrally over base of mandibles, with clypeo-pleurostomal lines divergent ventrally. Genae only slightly expanded posterior to eyes.

Antennae (Fig. 1). With 13 antennomeres, about two thirds as long as body length. Conspicuous placodeal sensilla present on F2 and following flagellomeres. F1 2.5× as long as wide. F2 2.8× as long as wide; about 1.3× as long as F1. Apical flagellomere 3.0× as long as wide.

Mesosoma (Figs. 3–5). Moderately convex in lateral view. Pronotum coriaceous to reticulate, with medial height about 0.3× height of lateral margin. Submedial pronotal pits transverse, deep, and clearly separated. Pronotal plate incomplete, with lateral sutures terminating long before reaching dorsal margin. Mesopleuron including speculum entirely striate-reticulate, with sculpture primarily reticulate but with conspicuous striae intermediate to cells of reticulate sculpture. Mesopleural triangle conspicuously impressed, with dense setae throughout. Mesoscutum strongly reticulate throughout, with sparse, scattered setae. Notauli incomplete, narrow, and poorly impressed, most apparent in posterior half of mesoscutum. Median mesoscutal impression conspicuous, strongly impressed in posterior third of mesoscutum. Mesoscutellar disc reticulate anteriorly and medially to rugose-reticulate around outer margins. Mesoscutellar foveae ovate-subtriangular; relatively long, occupying about anterior third of mesoscutellar disc; posterior margins poorly defined but distinctly divergent; without setae; smooth to reticulate within margins; separated by a broad subtriangular area. Metapleural sulcus meeting mesopleuron in dorsalmost third. Metapleuron coriaceous to rugose, more or less densely setose throughout. Propodeal carinae conspicuous, apparent as paired subparallel lateral carinae.

Wings (Fig. 6). Marginal cell of fore wing closed, 2.8× as long as wide; areolet conspicuous but veins weakly sclerotized. Distal margins with conspicuous marginal setae.

Metasoma (Fig. 1). Subequal to combined length of head and mesosoma. Second metasomal tergite with conspicuous anteromedial setose patch. Third and following metasomal tergites with dense micropunctuation throughout.

Male unknown.

Biology. Host unknown. Based on morphological similarities to other known Aulacideini (see diagnosis for *Soparia*), *S. oshensis* is probably associated with a plant in the families Asteraceae or Lamiaceae.

Distribution. Known only from Kyrgyzstan's Osh Region.

Remarks. While *S. oshensis* might at first seem to be an atypical species of *Aulacidea* due to the closed marginal cell and the presence of a setose patch on the second metasomal tergite, the striate-reticulate mesopleuron more closely resembles taxa in the aulacideine clade containing *Antistrophus*, *Liposthenes*, and related genera rather than taxa in the *Aulacidea-Isocolus* clade (see phylogeny in Ronquist *et al.* 2015). Regardless, *Soparia* does not fit within any currently defined genus in Aulacideini, including the current heterogeneous circumscriptions of *Aulacidea*, *Isocolus*, or *Antistrophus* (Melika 2006, Nieves-Aldrey 2022, Nastasi *et al.* 2024a, 2024b), thus requiring the establishment of a new genus.



FIGURES 7–8. *Panteliella fedtschenkoi* (Rübsaamen, 1896), female USNMENT 01823223. (7) Lateral habitus. (8) Dorsal mesosoma.

Panteliella Kieffer, 1901

(Figs. 7–14)

Pantelia Kieffer, 1901a

Panteliella Kieffer, 1901b

Vetustia Belizin, 1959

Endocaulonia Ionescu & Roman, 1960

Historical overview. *Panteliella* previously included two valid species: *P. bianchii* Vyrzhikovskaya, 1962 and *P. fedtschenkoi* (Rübsaamen, 1896). *Panteliella* was first described to accommodate *Aulax fedtschenkoi* (Rübsaamen, 1896), a species inducing small galls on leaves of *Phlomoides tuberosa* (L.) Moench (Lamiaceae: Lamioideae; synonym *Phlomis tuberosa* L.) (Kieffer 1901a, 1901b). Kieffer (1901a) first described this genus under the name *Pantelia*, but this name was preoccupied by an orthopteran genus; Kieffer (1901b) thus applied the replacement name *Panteliella* shortly thereafter.

In the following century, several authors described additional genera and species of herb gall wasps associated with *Phlomoides tuberosa* (L.) Moench, all of which have since been synonymized with *Panteliella fedtschenkoi*. Belizin (1959) described a morphologically similar species, *Vetustia investigata*, from galls in the inflorescence. Ionescu & Roman (1960) described another similar species, *Endocaulonia bicolor*, from cryptic stem galls. Quinlan (1968) examined *Panteliella* along with other cynipids then associated with *Phlomis* L., providing a brief redescription of *Panteliella fedtschenkoi* and treating *Vetustia investigata*, but did not include *Endocaulonia*. Nieves-Aldrey (1994) synonymized *Endocaulonia* with *Panteleilla*, without establishing synonyms at the species level. Melika (2006) synonymized *Vetustia investigata* and *Panteliella bicolor* with *P. fedtschenkoi*; the latter synonymy was not discussed beyond mentioning *P. bicolor* as a synonym of *P. fedtschenkoi*, although some discussion was given regarding the synonymy of *Vetustia investigata*.

No comprehensive revision has yet addressed all names included in *Panteliella*. After synonymies by Melika (2006) and Nieves-Aldrey (1994), only the species *P. bianchii* and *P. fedtschenkoi* remain valid, although the former species has not been mentioned in the literature aside from its original description (Vyrzhikovskaya, 1962). Considering the biologies of synonymized species, *P. fedtschenkoi* is currently hypothesized to induce galls on the leaves and in the stems and inflorescences (Melika 2006), which is highly atypical for a gall wasp species. Melika mentions several adult morphological characters that seem to differ depending on the plant organ from which the specimen was reared, particularly the body coloration and the distinction of the notauli. Melika also states that the number of antennomeres in the female varies from 13 to 14 in some specimens, and other characters, such as the dimensions of the marginal cell (there termed the radial cell), vary considerably.

Further complicating the taxonomy of *Panteliella* is differential treatments of synonymous taxa in phylogenetic studies. Liljeblad & Ronquist (1998) included *Panteliella bicolor* and *Vetustia investigata* in their morphological phylogenetic analysis, but they did not treat the type species *P. fedtschenkoi*. Ronquist *et al.* (2015) based their morphological analysis on Liljeblad & Ronquist's character set, apparently without considering the synonymies published by Melika (2006). The “*P. bicolor*” specimens studied in these analyses were reared from stems of the known host plant species in Hungary; the same stems apparently also yielded specimens of *Aulacidea phlomica* Belizin, 1959 (Ronquist, pers. comm.).

Altogether, *P. fedtschenkoi* requires further revision, to determine the conspecificity of species currently treated as synonyms, and we presently expect that multiple valid species will be identified among the broad concept of *P. fedtschenkoi* employed in prior studies (e.g., Melika 2006). The synonymy of *Panteliella*, *Endocaulonia*, and *Vetustia* should also be verified through further study. To facilitate continuing work on *Panteliella*, we redescribe the genus below, and also provide a redescription of *P. fedtschenkoi*. The specimen collected in Kyrgyzstan substantially differs from the *P. fedtschenkoi* we examined, justifying its establishment as a new species. We describe it here as *P. rugosa* Nastasi sp. nov. Additionally, the species *P. bianchii* has only been mentioned in its original description and has not been treated by any further studies despite several subsequent works concerning *Panteliella* (e.g., Melika 2006, Nieves-Aldrey 2022). We have not examined the type material, but based on its original description, *P. bianchii* appears to represent a valid species. To assist in resolving taxonomic issues in *Panteliella*, we provide a key to the three known species, including *P. bianchii* based on characters present in its original description. We also provide a translation of the original description of *P. bianchii* (see below species treatment). Lastly, we provide a table of diagnostic characters for the three valid species we recognize as well as the two species presently synonymized

with *P. fedtschenkoi* (Table 1). Given the high degree of morphological divergence of *Vetustia investigata* (currently placed as a synonym of *P. fedtschenkoi*; see below species treatment and Table 1), it is evident that our description and diagnosis for *Panteliella* will likely require revision after type material of these species can be examined.

More broadly, the diagnostic characters for *Panteliella* given in the literature vary substantially and complicate the recognition of the genus. For instance, in the last published generic key (Nieves-Aldrey 2022), a diagnostic character for *Panteliella* is the lack of defined lateral propodeal carinae. However, in all specimens we examined here, there are distinct lateral propodeal carinae. To address these conflicting elements, we provide a redescription, based on the material we examined in this study, particularly isotypic specimens of *P. fedtschenkoi* (see below). As mentioned above, further studies will be needed to resolve the generic and specific limits of *Panteliella*.

TABLE 1. Major characters of valid *Panteliella* species and synonyms of *P. fedtschenkoi*. *: Material not examined here; characters based on treatments by Belizin (1959), Ionescu & Roman (1960), Vyrzhikovskaya (1962), Quinlan (1968), Nieves-Aldrey (1994), Liljeblad & Ronquist (1998), Melika (2006).

Species	♀ # antennomeres	F2:F1 length	Notauli	Mesoscutum rugae	Gall organ
<i>P. bianchii</i> *	14	F1 longer	Incomplete(?)	Absent	Unknown
<i>P. fedtschenkoi</i>	14	Subequal	Incomplete	Absent	Leaf
<i>P. rugosa</i>	13	Subequal	Incomplete	Present	Unknown
<i>Endocaulonia bicolor</i> *	14	Subequal	Incomplete	Absent	Stem
<i>Vetustia investigata</i> *	12	F1 longer	Complete	Absent	Inflorescence

Diagnosis. *Panteliella*, as presently circumscribed, can be easily distinguished from other Aulacideini genera by the following combination of characters: Fore wing with marginal cell open; mesopleuron sculpture almost entirely striae (Fig. 13); second metasomal tergite without conspicuous patch of setae (Fig. 9); clypeus large, broadly projecting over base of mandibles and with clypeo-pleurostomal lines strongly divergent ventrally (Fig. 10); notauli incomplete, poorly impressed, more or less indistinct (Figs. 8; 11), apparent only as short longitudinal rugae in posterior mesoscutum.

Panteliella is closest morphologically to *Liposthenes* Förster, 1869 (Nieves-Aldrey 2022), but is easily separated by the notauli (complete and distinctly impressed in *Liposthenes*). *Panteliella* is also morphologically similar to some *Antistrophus* species based on the state of the notauli, open marginal cell, and lack of a distinct setose patch on the second metasomal tergite (Nastasi *et al.* 2024a, 2024b). However, the two genera are easily differentiated by the mesopleuron sculpture (always with some amount of perceptible reticulate sculpture in *Antistrophus*) and by the clypeus, which is smaller and does not strongly project ventrally in *Antistrophus*.

Redescription. Head mostly orangish brown or entirely black, mesosoma black, and metasoma dark brown to black. Head subtrapezoidal in anterior view, conspicuously wider than tall. Facial radiating striae always poorly impressed and incomplete, only reaching slightly beyond clypeus. POL much longer than OOL. Malar space much shorter than height of compound eye. Clypeus large, broadly projecting over base of mandibles, and with clypeo-pleurostomal lines strongly divergent ventrally. Female antennae with 13 or 14 antennomeres; males (not examined here) reportedly with 14 or 15. Female F1 equal to F2 (apparently also in males). Mesosoma in lateral view convex to conspicuously angled posteriorly. Lateral pronotum without rugose sculpture (strong rugose sculpture often present in other Aulacideini such as some *Antistrophus* or *Liposthenes*). Pronotal plate incomplete but with lateral sutures terminating only shortly before reaching mesoscutum. Mesopleuron almost entirely striae, with a very small ventral area of reticulate sculpture. Mesoscutum coriaceous to reticulate, occasionally with some degree of perceptible rugose sculpture. Notauli incomplete, narrow, and poorly impressed, most apparent in posterior third of mesoscutum. Median mesoscutal impression not apparent. Mesoscutellar foveae ovate to subquadrate, about one quarter as long as mesoscutellar disc and with posterior margins poorly defined. Propodeum with or without a conspicuous pair of lateral carinae (lateral carinae absent in specimens examined by Nieves-Aldrey [2022], in which only a strong median carina is apparent). Fore wing with marginal cell open, with vein R1 indistinctly reaching fore

wing margin, and with conspicuous marginal setae. Areolet absent. Metasoma with conspicuous micropunctuation at least on third and following metasomal tergites. Second metasomal tergite without setose patch, at most with a few scattered setae.

Biology. *Panteliella fedtschenkoi* induces galls on *Phlomoides tuberosa* (Lamiaceae). The genus was originally described for a species inducing monothalamous galls on the leaves, but genera currently synonymized with *Panteliella* were described from galls in the inflorescence and cryptic galls in the stems (Belizin 1959, Ionescu & Roman 1960). The host plants of *P. bianchii* and *P. rugosa* sp. nov. are unknown.

Distribution. *Panteliella* has been recorded throughout Europe and parts of continental Asia including Mongolia (Nieves-Aldrey 1994, Belizin 1959, Quinlan 1968, Melika 2006). We document the genus from Kyrgyzstan for the first time (see treatment of *P. rugosa* Nastasi sp. nov. below).

Key to the species of *Panteliella* Kieffer, 1901

1. Mesoscutum with conspicuous, abundant transverse rugae (Fig. 11). Female antennae with 13 antennomeres (Fig. 9). Mesoscutellar foveae (Fig. 12) short, occupying only anterior quarter of mesoscutellar disc, and subrectangular. *rugosa* Nastasi sp. nov.
- Mesoscutum without apparent transverse rugae (Fig. 8). Female antennae with 14 antennomeres (Fig. 7). Mesoscutellar foveae (Fig. 8) longer and ovate. 2
2. Female F1 subequal to F2. Head at least partly lighter in color than mesosoma, particularly on face and genae (Fig. 7). Mesoscutellar disc subcircular and strongly sculptured. *fedtschenkoi* (Rübsaamen, 1896)
- Female F1 longer than F2. Head entirely black, concolorous with mesosoma. Mesoscutellar disc triangular and weakly sculptured. *bianchii* Vyrzhikovskaya, 1962*

* = We include *Panteliella bianchii* in the key based on characters given in the original description (see translation below). Examination of the type of *P. bianchii* will be needed to confirm the diagnostic characters given here.

Panteliella fedtschenkoi (Rübsaamen, 1896)

(Figs. 6–7)

Aulax fedtschenkoi Rübsaamen, 1896

Pantelia fedtschenkoi (Rübsaamen) Kieffer, 1901a

Panteliella fedtschenkoi (Rübsaamen) Kieffer, 1901b

Endocaulonia bicolor Ionescu & Roman, 1960

Panteliella bicolor (Ionescu & Roman) Nieves-Aldrey, 1994

Vetustia investigata Belizin, 1959

Material examined. Two females, USNM 01823222, 01823223, both with same labels given verbatim here: “Bijouk-Onlar, Krim.” / “Cut out of type galls by Weld 1929” / “From Vienna Museum, 1929” / “*Panteliella fedtschenkoi* (Rübsaam.)” / USNM barcode label. The labels report the locality only as “Bijouk-Onlar, Krim.”, which likely refers to Bijuk-Onlar, a former name of the settlement Oktyabrsk in the Crimean Peninsula. Labels that were evidently added later correspond to Weld’s (1930) observations and indicate that the specimens were dissected from galls collected and preserved alongside the type series of this species. Both specimens are in relatively good condition, with one specimen missing only an antenna and the other mostly intact except for undeveloped wings.

Redescription of female (Fig. 7). Body 1.2 mm in length (n = 2). Coloration clearly faded since initial preservation, but coloration of head much lighter brownish than that of mesosoma and metasoma, especially on face. Antennae reddish yellow. Wing veins pale brown. Legs more or less orangish throughout.

Head. In dorsal view 1.9× as wide as long; in anterior view subtrapezoidal and 1.4× as wide as tall. Sculpture excluding weak facial radiating striae entirely coriaceous. POL:LOL:OOL:DLO in holotype measuring 15:7:7:4. Toruli situated about mid-height of eyes. Malar space 0.6× as long as compound eye in anterior view. Facial radiating striae incomplete, very poorly impressed, apparent as indistinct rugae emanating for a short distance from the clypeus. Clypeus large, broadly projecting ventrally over base of mandibles, and with clypeo-pleurostomal lines strongly divergent ventrally. Genae only slightly expanded posterior to eyes.

Antennae (Fig. 7). With 14 antennomeres, about two thirds as long as body length. Conspicuous placodeal sensilla present on F2 and following flagellomeres. Pedicel about as long as F1. F1 2.0× as long as wide. F2 1.8× as long as wide; about 1.0× as long as F1. Apical flagellomere 2.1× as long as wide.

Mesosoma (Figs. 7–8). Strongly convex in lateral view. Pronotum coriaceous, with medial height about 0.3× height of lateral margin. Submedial pronotal pits transverse, deep, and clearly separated. Pronotal plate incomplete, with lateral sutures terminating only shortly before reaching mesoscutum. Mesopleuron almost entirely striate, with a very small ventral area of reticulate sculpture. Mesopleural triangle conspicuously impressed, with only a few scattered setae anteriorly. Mesoscutum mostly weakly coriaceous, with a few conspicuous longitudinal rugae apparent for a short distance anterior to scutellar margin, with only a few sparse, scattered setae. Notauli incomplete, inconspicuously impressed; apparent only as short longitudinal rugae in posterior third of mesoscutum. Median mesoscutal impression not apparent but mesoscutum very slightly impressed posteromedially. Mesoscutellar disc mostly reticulate, with conspicuous longitudinal rugae anteriorly and rugose-reticulate toward outer margins. Mesoscutellar foveae ovate; relatively short, about one quarter as long as mesoscutellar disc; posterior margins poorly defined but strongly divergent; without setae; rugose within margins; separated by a broad subtriangular area. Metapleural sulcus meeting mesopleuron in dorsal third. Metapleuron coriaceous to rugose, more or less moderately setose throughout. Propodeal carinae conspicuous, apparent as paired subparallel lateral carinae, with strong sculpture between them producing a faint indication of a medial carina.

Fore wing (Fig. 7). Hyaline and setose throughout. Marginal cell open, 2.9× as long as wide, with vein R1 indistinctly reaching fore wing margin. Areolet absent. Distal margin with conspicuous marginal setae.

Metasoma. Metasoma slightly shorter than combined length of head and mesosoma. Second metasomal tergite without conspicuous anteromedial setose patch. Third and following metasomal tergites with sparse micropunctuation throughout.

Redescription of gall. On the adaxial leaves of *Phlomoides tuberosa*. Conspicuous, solitary, semideciduous outgrowths of the leaf, 2.0–4.0 mm in diameter. Monothalamous. Shape spherical. Surface slightly rugose, with dense, moderately long pilosity. Color green when fresh to pink or brown when mature or dry. While *Panteliella fedtschenkoi* has been mentioned to induce galls in the inflorescence or stems, these records almost certainly correspond to distinct species (see remarks below).

Remarks. Several authors have treated *Panteliella fedtschenkoi* since its description, often disagreeing on diagnostic characters (see remarks for *Panteliella* above). Weld (1930) redescribed *Panteliella fedtschenkoi* from two specimens dissected from galls of the type series as the original description was insufficient. We examined Weld's material (see above) and redescribe the species in line with characters included in our description of *P. rugosa* Nastasi sp. nov. (below). As mentioned above, further study of material of this species is badly needed to better understand its limits; Melika's (2006) treatment of *P. fedtschenkoi* probably encapsulates multiple species (see remarks for *Panteliella* above). Given that the material we examined here was dissected by Weld from galls preserved alongside Rübsaamen's type material (Weld 1930), and that the known adult types of the species are incomplete and mounted on slides (Quinlan 1968, Nieves-Aldrey 1994), we believe that our treatment here best represents the species hypothesis as intended by Rübsaamen.

Panteliella rugosa Nastasi sp. nov.

urn:lsid:zoobank.org:act:BFD917CC-CDC3-4755-B88D-07A212879EDE

(Figs. 9–14)

Material examined. Holotype female: INHS Insect Collection 288137. Kyrgyzstan: Osh Region, Ikazak, 2 km east of junction with Koksu River, 39°42'51" N, 73°46'30" E (approximately 39.714, 73.775 in decimal degrees). 3100m elevation. Collected 9 July 2000, by vacuum. Field code 00-092-08. C. H. Dietrich leg.

Etymology. Named for the abundant rugose sculpture on the mesoscutum of this species. Noun in apposition.

Description. Female (Fig. 9)–Body 1.5 mm in length. Coloration of head mostly orangish brown, with occiput dark brown; mesosoma more or less entirely black; metasoma dark reddish brown. Mandibles yellow. Antennae orangish brown, with scape and pedicel slightly darker than following antennomeres. Wing veins brown. Legs yellow except coxae and femora light brown proximally to yellow distally and apical tarsomeres light brown.

Head (Fig. 10). In dorsal view 1.8× as wide as long; in anterior view subtrapezoidal and 1.2× as wide as tall. Sculpture excluding facial radiating striae entirely coriaceous. POL:LOL:OOL:DLO in holotype measuring

13:6:8:3. Toruli situated about mid-height of eyes. Malar space about $0.75\times$ as long as compound eye in anterior view. Facial radiating striae incomplete, poorly impressed, apparent as weak striations emanating for a short distance from the clypeus. Clypeus large, broadly projecting ventrally over base of mandibles, and with clypeo-pleurostomal lines strongly divergent ventrally. Genae only slightly expanded posterior to eyes.

Antennae (Fig. 9). With 13 antennomeres, about two thirds as long as body length. Conspicuous placodeal sensilla present on F2 and following flagellomeres. Pedicel shorter than F1. F1 $2.3\times$ as long as wide. F2 $2.6\times$ as long as wide; about $1.0\times$ as long as F1. Apical flagellomere $3.7\times$ as long as wide.

Mesosoma (Figs. 11–13). In lateral view somewhat convex anteriorly but conspicuously angled in posterior three quarters. Pronotum mostly coriaceous, with some apparent rugose sculpture lateral to pronotal plate; with medial height about $0.3\times$ height of lateral margin. Submedial pronotal pits transverse, deep, and clearly separated. Pronotal plate incomplete, with lateral sutures terminating only shortly before reaching mesoscutum. Mesopleuron almost entirely striate, with a very small ventral area of reticulate sculpture. Mesopleural triangle conspicuously impressed, densely setose throughout. Mesoscutum strongly reticulate with abundant transverse rugae, with only a few sparse, scattered setae. Notauli incomplete and inconspicuous; apparent only as short longitudinal rugae in posterior third of mesoscutum. Median mesoscutal impression inconspicuous. Mesoscutellar disc entirely rugose-reticulate, with conspicuous rugae anteriorly. Mesoscutellar foveae ovate; relatively short, about one quarter as long as mesoscutellar disc; posterior margins poorly defined but strongly divergent; without setae; rugose within margins; separated by a broad subtriangular area. Metapleural sulcus meeting mesopleuron in dorsal third. Metapleuron coriaceous to rugose, more or less moderately setose throughout. Propodeal carinae conspicuous, apparent as paired subparallel lateral carinae.

Fore wing (Fig. 14). Hyaline and setose throughout. Marginal cell open, $3.4\times$ as long as wide, with vein R1 indistinctly reaching fore wing margin. Areolet absent. Distal margin with conspicuous marginal setae.

Metasoma (Fig. 9). Slightly longer than combined length of head and mesosoma. Second metasomal tergite with sparse micropunctuation in posterior third. Third and following metasomal tergites with sparse micropunctuation throughout.

Male—Unknown.

Remarks. We examined *Panteliella fedtschenkoi* and reviewed descriptions and redescriptions of its synonyms (Belizin 1959, Ionescu & Roman 1960, Quinlan 1968) and found that our *P. rugosa* is morphologically distinct from these species (Table 1). While the host of *P. rugosa* is not yet known, it is probably associated with *Phlomoides tuberosa* or a related species, as is the case for all taxa currently placed within *Panteliella*.

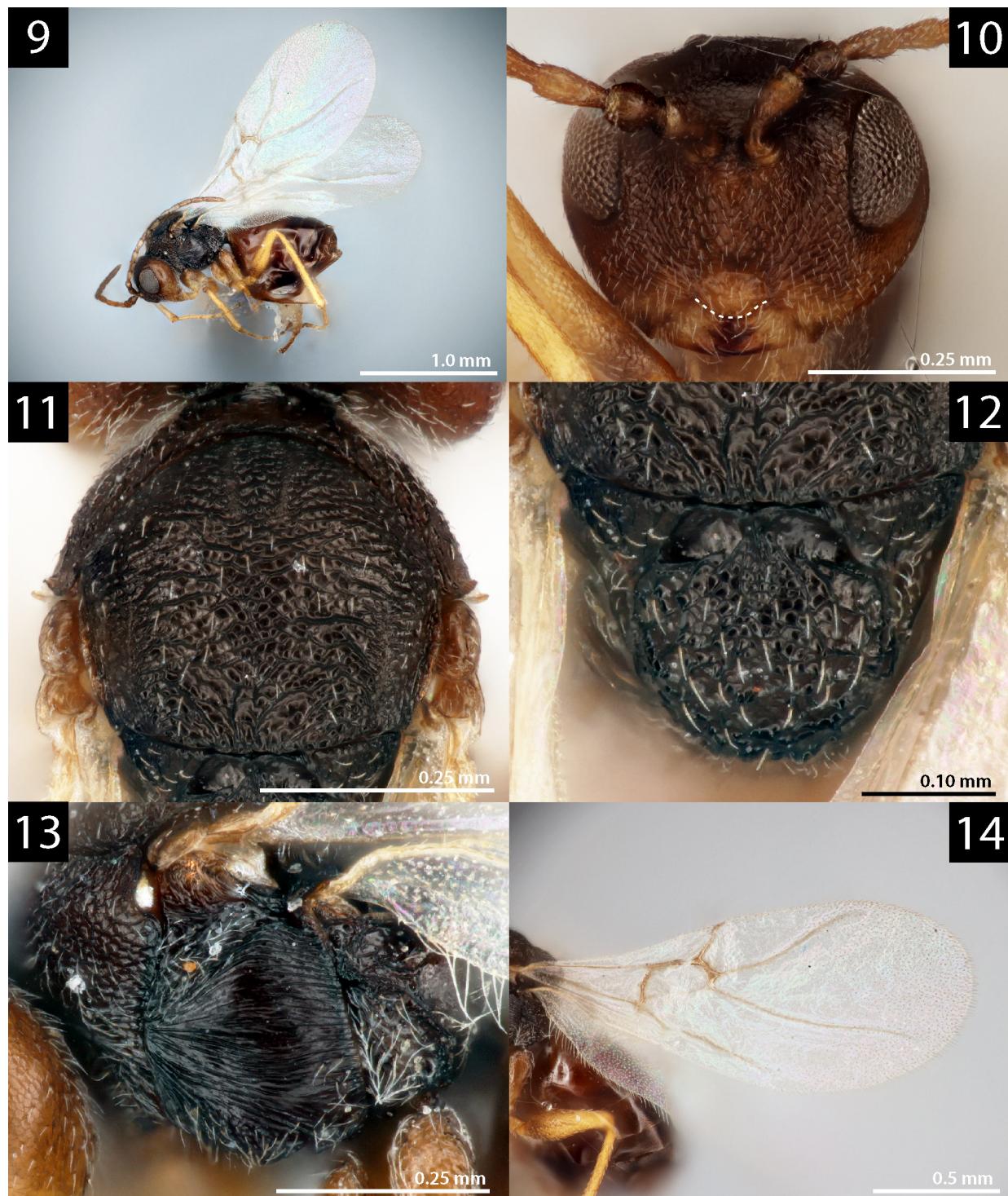
Panteliella bianchii Vyrzhikovskaya, 1962

Description translated from Vyrzhikovskaya (1962). Female—Body black. Head wider than high and slightly wider than mesosoma. Occiput and vertex smooth and shining. Face with slight medial elevation. Facial radiating striae apparent but weakly indicated. Genae coriaceous. Malar space slightly longer than half the compound eye length. Antennae rufous, with 14 antennomeres, slightly expanded distally. F1 slightly longer than F2. Pronotum sculpture reticulate. Mesoscutum weakly sculptured; nearly smooth. Notauli conspicuous [length of conspicuous portion unclear]. Mesopleuron at least partly striate [described as smooth to striate but degree of either sculpture type unclear]. Mesoscutellar disc weakly sculptured, apparently strongly triangular, and with conspicuous, long mesoscutellar foveae; area within foveae smooth and unsculptured. Wings hyaline; veins brown; basal vein and radius strongly thickened; marginal cell open; areolet absent. Legs yellow-brown. Metasoma shiny; brownish in color. Second metasomal tergite occupying about half metasoma length. Ventral spine short, slightly longer than basal width.

Host. Unknown.

Distribution. Described from the vicinity of Leningrad (Russia).

Remarks. Vyrzhikovskaya (1962) notes that *P. bianchii* differs from *P. fedtschenkoi* by the weak sculpture of the mesoscutum, the longer mesoscutellar foveae, and the overall shape of the mesoscutellum. However, an in-depth study of the type material is needed to substantiate these characters and those given in the above redescription and key. We have not yet been able to locate the type of *P. bianchii*; we contacted the Zoological Institute at the Russian Academy of Science (St. Petersburg, Russia), who informed us that Vyrzhikovskaya's types, including *P. bianchii*, were not present in their collection (Sofya Tyulina, pers. comm., September 2024). While the host of *Panteliella bianchii* is not known, it may be associated with *Phlomoides tuberosa* or a related plant species.



FIGURES 9–14. *Panteliella rugosa* Nastasi sp. nov. All images show holotype female INHS Insect Collection 288137. (9) Lateral habitus. (10) Head in anterior view; dotted line indicates ventral margin of clypeus. (11) Mesoscutum in dorsal view. (12) Scutellum in dorsal view. (13) Mesopleuron in lateral view. (14) Fore wing.

***Isocolus barakus* Nastasi sp. nov.**

urn:lsid:zoobank.org:act:1EEB77F3-1302-45A7-97A9-1F829EAC8A12

Material examined. One female: INHS Insect Collection 288135. Kyrgyzstan: Chuy, Bulak, 9 km west of Ak-Tuz, 42°52'47" N, 76°2'13" E (approximately 42.880, 76.040 in decimal degrees). 2180–3400 m elevation. Collected 26 July 2000, by vacuum. Field code 00-114-03. C. H. Dietrich coll.

Etymology. From the Kyrgyz word бапак (phoneticized as “barak”), meaning “sheet” or “plate” and referring to the atypical presentation of the pronotal plate in this species. Noun in apposition.

Diagnosis. *Isocolus barakus* can be easily distinguished from other *Isocolus* species by the pronotal plate, which is incomplete but with the dorsal portion conspicuously defined laterally in *I. barakus* (Fig. 17) but incomplete and poorly developed in other *Isocolus* species (see remarks below). The following combination of characters further separates *I. barakus* from other *Isocolus* species: Mesoscutum (Fig. 20) entirely reticulate, without perceptible transverse sculpture; female with 13 antennomeres, with F2 conspicuously longer than F1 (Fig. 18) and without placodeal sensilla on F2; facial radiating striae complete and well-defined (Fig. 16); notauli complete (Fig. 20); second metasomal tergite without conspicuous setose patch (Fig. 15); second metasomal tergite without punctuation.

Description of female (Fig. 15). Body 2.1 mm in length. Coloration of head and mesosoma entirely black; metasoma reddish brown. Mandibles reddish brown. Antennae reddish brown, with scape, pedicel, F1, and some apical flagellomeres much darker. Wing veins brown. Legs yellow except coxae, trochanters, and femora brown proximally to yellow distally and apical tarsomeres brown.

Head (Fig. 16). In anterior view slightly subtrapezoidal, 1.2× as wide as tall. Sculpture excluding facial radiating striae coriaceous to reticulate throughout. POL:LOL:OOL:DLO in holotype measuring 11:9:11:4. Malar space 0.6× as long as compound eye in anterior view. Facial radiating striae complete, conspicuously impressed and reaching from clypeus to ventral eye margin. Clypeus subtrapezoidal, moderately projecting ventrally over base of mandibles, and with clypeo-pleurostomal lines strongly divergent ventrally. Genae only slightly expanded posterior to eyes.

Antennae (Figs. 15; 18). With 13 antennomeres, about two thirds as long as body length. Conspicuous placodeal sensilla present on F3 and following flagellomeres. F1 2.7× as long as wide. F2 2.8× as long as wide; 1.3× as long as F1.

Mesosoma (Figs. 17; 19–21). Moderately convex in lateral view. Pronotum coriaceous to reticulate, with some indistinct striation posteroventrally. Pronotal plate incomplete but well developed, with lateral sutures nearly reaching anterior margin of mesoscutum. Mesopleuron sculpture entirely striate. Mesopleural triangle conspicuously impressed, with dense setae throughout. Mesoscutum coriaceous throughout, with sparse, scattered setae. Notauli complete and narrow throughout. Median mesoscutal impression indistinct. Mesoscutellar disc reticulate anteriorly and medially to rugose-reticulate around outer margins. Mesoscutellar foveae conspicuously impressed, apparent as ovate-subrectangular impressions occupying about anterior third of mesoscutellar disc; smooth to rugose within margins; separated by a broad subtriangular area. Metapleural sulcus meeting mesopleuron around medial third. Propodeal carinae conspicuous, apparent as paired subparallel lateral carinae.

Wings (Fig. 15). Hyaline and setose throughout. Fore wing with marginal cell open, 2.7× as long as wide, with vein R1 just about meeting wing margin; areolet conspicuous. Distal margins with conspicuous marginal setae.

Metasoma (Fig. 15). Slightly longer than combined length of head and mesosoma. Second metasomal tergite without conspicuous setose patch, with only a few scattered setae. Third and following metasomal tergites with dense micropunctuation throughout.

Biology. Host unknown.

Remarks. This specimen would, at first, appear to represent a species of *Isocolus* Förster, based on the open marginal cell, slightly projecting clypeus, entirely striate mesopleuron, and having 13 antennomeres in females. However, the pronotal plate is conspicuously defined laterally and nearly complete, with the lateral sutures nearly reaching the anterior mesoscutum but not producing a raised plate (Fig. 17, arrows). The strongly defined but incomplete pronotal plate is typical of some Aulacideini, namely *Liposthenes* and *Panteliella* (Nieves-Aldrey 2022), but these species vary considerably from *I. barakus*, particularly in the structures of the face and mesoscutum, among other characters (Nieves-Aldrey 2022). Additionally, the mesoscutum in most *Isocolus* species exhibits conspicuous raised, transverse sculpture, but this is not the case in *I. barakus*. As *I. barakus* does not exhibit obvious synapomorphies among Aulacideini, but rather possesses plesiomorphic characters in a unique combination, we prefer to place it in *Isocolus* until further revisionary studies can be done. *Isocolus barakus* does not strongly disagree with general diagnostic characters of *Isocolus* despite several atypical characters, but the genus has not been recently revised, and the diagnostic characters given in the literature (e.g., Nieves-Aldrey 1994, Melika 2006, Nieves Aldrey 2022) require further validation.



FIGURES 15–21. *Isocolus barakus* Nastasi sp. nov. All images show holotype female INHS Insect Collection 288135. (9) Lateral habitus. (10) Head in anterior view; dotted line indicates ventral margin of clypeus. (11) Pronotum in anterior view; arrows indicate conspicuously defined range of pronotal lateral suture. (12) Proximal antennomeres. (13) Mesopleuron in lateral view. (14) Mesoscutum in dorsal view. (15) Scutellum in dorsal view; posterior scutellum (partially covered by wings and thus clouded posteriorly in image).

Key to the Aulacideini genera of Kyrgyzstan

We provide the following key to allow for the separation of all Aulacideini genera known from Kyrgyzstan. Specimens may be identified as Aulacideini using the identification key in Buffington et al. (2020), although some updated diagnostic characters were provided by Nastasi et al. (2024a) to prevent the exclusion of taxa with reticulate sculpture on the mesopleuron (e.g., *Soparia* Nastasi gen. nov.).

1.	Fore wing marginal cell closed (Fig. 6)	2
-	Fore wing marginal cell open (Fig. 14)	3
2.	Mesopleuron sculpture entirely striae-reticulate (Fig. 5). Notauli incomplete and weakly impressed, most conspicuous in posterior half of mesoscutum (Fig. 3)	<i>Soparia</i> Nastasi gen. nov.
-	Mesopleuron sculpture mostly or entirely striae; at most with some reticulate sculpture apparent in ventral third. Notauli complete, deeply impressed across entire mesoscutum*.	<i>Aulacidea</i> Ashmead, 1897
3.	Notauli conspicuous and strongly impressed (Fig. 20). Clypeus only slightly projecting ventrally over base of mandibles (Fig. 16)	<i>Isocolus</i> Förster, 1869
-	Notauli inconspicuous to weakly impressed (Fig. 11). Clypeus broadly projecting ventrally over base of mandibles (Fig. 10)	<i>Panteliella</i> Kieffer, 1901

* = Notauli complete in both species known from Kyrgyzstan (*Aulacidea acroptilonica* Tyurebaev, 1972 and *A. serratulae* Diakontschuk, 1984) but incomplete in some species known from other geographic regions.

Discussion

Our description of a new genus and three new species of Aulacideini suggests that the herb gall wasp fauna of Kyrgyzstan warrants further study. While many studies have investigated the diversity of gall wasps in the eastern Palearctic, only a handful specifically mention the nation of Kyrgyzstan in relation to herb gallers (Melika 2006, Zerova *et al.* 1988, Kovalev & Diakontschuk 1986).

Further study of type material for Aulacideini described from the eastern Palearctic realm will greatly improve our ability to recognize these species, especially as generic and tribal revisions continue to impact the global gall wasp fauna (Ronquist *et al.* 2015, Nieves-Aldrey 2022). While we find here that *Panteliella bianchii* likely comprises a species distinct from other *Panteliella* as treated here, study of Vyrzhikovskaya's type material will be necessary. More broadly, the same can be said for other morphologically or biologically atypical taxa from the eastern Palearctic region. Numerous species currently placed in *Aulacidea*, especially species described by Diakontschuk (Melika 2006) and several species recently described from Iran (*A. koeiana*, *A. loresitanica*, and *A. piroziae*; Tavakoli *et al.* 2022) do not resemble the better-known western European species, and thus would likely benefit from further revision. The numerous genera associated with Lamiaceae, including *Panteliella* as discussed above, would also benefit from continuing revision (Nieves-Aldrey 2022). As noted elsewhere, a complete generic revision of Aulacideini will be needed to fully understand proper species placement in the tribe (Melika 2006, Nieves-Aldrey 2022, Nastasi & Deans 2024).

Acknowledgments

George Melika assisted in accessing literature on the Russian gall wasp fauna. José Luis Nieves-Aldrey and Fredrik Ronquist provided valuable commentary on the genus *Panteliella* and other topics related to Aulacideini. Sofya Tyulina communicated with us regarding the type of *Panteliella bianchii*. Karina Zhuzenova assisted in determining the correct Kyrgyz terms for etymological purposes. Tommy McElrath, Matt Buffington, and Cecilia Escobar assisted with arranging specimen loans. Charles Davis, Cecil Smith, John Tooker, Heather Hines, and Laura Porturas have provided excellent support in our ongoing studies of herb gall wasps.

This material is based upon work supported by the National Science Foundation under Grant Nos. DEB-1856626 and DEB-2338008. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. LFN was supported by two awards from the Society of Systematic Biologists: Mini-ARTS and the Graduate Student Research Award.

References

Ashmead, W.H. (1897) Description of Some New Genera in the Family Cynipidae. *Psyche*, 8, 67–69.
<https://doi.org/10.1155/1897/60546>

Belizin, V.I. (1959) Gall wasps of the tribe Aylaxini (Hymenoptera, Cynipoidea) new for the fauna of the U. S. S. R.

Entomologicheskoe Obozrenie, 38, 662–674.

Buffington, M.L., Forshage, M., Liljeblad, J., Tang, C.T. & 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>

Deans, A.R., Nastasi, L.F. & Davis, C.K. (2024) GallOnt: An ontology for plant gall phenotypes. *Biodiversity Data Journal*, 12, e128585.
<https://doi.org/10.3897/BDJ.12.e128585>

Deans, A.R., Nastasi, L.F. & Montelongo, D.C. (2023) Glossary of gall terms. Version 7. Available from: <https://doi.org/10.26207/22e9-ck06> (accessed 5 July 2024)

Diakontschuk, L.A. (1984) New species of Cynipidae (Cynipidae, Hymenoptera) from Georgia. *Vestnik Zoologii*, 3, 74–77. [in Russian]

Förster, A. (1869) Ueber die Gallwespen. *Verhandlungen der k.k. Zoologisch-botanischen Gesellschaft in Wien*, 19, 325–370.

International Commission on Zoological Nomenclature (1999) *International Code Of Zoological Nomenclature*. The International Trust for Zoological Nomenclature, London, 306 pp.

Ionescu, M.A. & Roman, N. (1960) Un genre nouveau de Cynipides gallocoles *Endocaulonia bicolor* n. g., n. sp. (Hymenoptera, Cynipoidea). *Revue de Biologie Academiei Republicii Populare Romine Bucaresti*, 5 (3), 221–225.

Kieffer, J.J. (1901a) *Monographie des Cynipides d'Europe et d'Algérie: Les Cynipides*. Froment-Dubosclard, Paris, 687 pp.

Kieffer, J.J. (1901b) Synopsis de Zoocecidies d'Europe. *Annales de la Société Entomologique de France*, 1901, 233–579.
<https://doi.org/10.1080/21686351.1901.12279879>

Kovalev, O.V. & Diakontschuk, L.A. (1986) A redescription of *Aulacidea acroptilonica* (Cynipidae, Hymenoptera). *Vestnik Zoologii*, 2, 16–19. [in Russian]

Liljeblad, J. & Ronquist, F. (1998) A phylogenetic analysis of higher-level gall wasp relationships (Hymenoptera: Cynipidae). *Systematic Entomology*, 23 (3), 229–252.
<https://doi.org/10.1046/j.1365-3113.1998.00053.x>

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

Nastasi, L.F., Buffington, M.L., Davis, C.K. & Deans, A.R. (2024a) 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. & 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, e68558
<https://doi.org/10.3897/BDJ.9.e68558>

Nastasi, L.F. & Deans, A.R. (2024) *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., Tooker, J.F., Davis, C.K., Smith, C.N., Frey, T.S., Hatfield, M.J., Presnall, T.M., Hines, H.M. & Deans, A.R. (2024b) 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. (1994) Revision of West-European Genera of the Tribe Aylacini Ashmead (Hymenoptera, Cynipidae). *Journal of Hymenoptera Research*, 3, 175–206.

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 (3), 393–413.
<https://doi.org/10.11646/zootaxa.5155.3.5>

PATO Curators (2023) Phenotype and Trait Ontology. Available from: <https://github.com/pato-ontology/pato/> (accessed 9 May 2024)

Quinlan, J. (1968) Cynipinae (Hymenoptera) occurring on *Phlomis* L. *Transactions of the Royal Entomological Society of London*, 120, 275–286.
<https://doi.org/10.1111/j.1365-2311.1968.tb00339.x>

Riley, C.V. & Walsh, B. (1869) The *Lygodesmia* Pea-gall. *American Entomologist*, 2, 73–74.

Ronquist, F., Nieves-Aldrey, J.L., Buffington, M.L., Liu, Z., Liljeblad, J. & 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>

Rübsaamen, E.H. (1896) Über russische Zoocecidien und deren Erzeuger. *Bulletin de la Société impériale des naturalistes de Moscou*, 3, 396–481.

Tavakoli, M., Stone, G.N., Pujade-Villar, J. & 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>

Tyurebaev, S.S. (1972) Gall-forming insects attacking Russian knapweed in the middle reaches of the R. Irtysh. *Vestnik Sel'skokhozyaistvennoi Nauki Kazakhskoi SSR*, 15 (6), 52–53.

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. [in Russian]

Weld, L.H. (1930) Notes on types (Hymenoptera: Cynipidae). *Proceedings of the Entomological Society of Washington*, 32 (8), 137–144.

Yoder, M.J., Mikó, I., Seltmann, K.C., Bertone, M.A. & Deans, A.R. (2010) A gross anatomy ontology for Hymenoptera. *PLoS ONE*, 5 (12), e15991.
<https://doi.org/10.1371/journal.pone.0015991>

Zerova, M.D., Diakontschuk, L.A. & Ermolenko, V.M. (1988) *Gallmaker insects of the European part of the USSR*. Naukova dumka, Kiev, pp. 1–159. [in Russian]