

DIVERSITY OF THE GALL-INDUCING CYNIPIDAE ON *QUERCUS VIRGILIANA* IN CENTRAL DALMATIA, CROATIA

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The cynipid gall wasps (Hymenoptera: Cynipidae) are among the main insects associated with oaks of the genus *Quercus*. In the tissues of the host plant, they form galls, specialized structures that provide shelter and nutrients for the developing insect larvae. The aim of this study was to determine the oak gall wasp community of the species *Quercus virgiliana*. The galls were collected from oak buds, leaves, cupulae and catkins in the Lepenica region (Central Dalmatia) in the years 2023–2024. The collected galls were dissected and observed under a stereomicroscope to examine their morphological characteristics as well as larvae, pupae and/or adult wasps. With 17 recorded species, *Andricus* is by far the largest genus, followed by *Neuroterus* with 3 species, *Cynips* with 2 species and a single species from the genus *Biorhiza*. We identified 18 types of galls, with bud galls being the most common and conspicuous, followed by leaf, cupula and catkin galls.

Key words: Cynipidae, gall wasps, *Quercus virgiliana*, gall morphology

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Ose šiškarice (Hymenoptera: Cynipidae) među glavnim su kukcima povezanim s hrastovima iz roda *Quercus*. U tkivima biljke domaćina formiraju šiške kao specijalizirane strukture koje pružaju zaštitu i hranjive tvari ličinkama u razvoju. Cilj ovog istraživanja bio je utvrditi raznolikost hrastovih osa šiškarica specijaliziranih za formiranje šiški na vrsti *Quercus virgiliana*. Uzorci su sakupljeni na području Lepenice (Srednja Dalmacija) s hrastovih pupova, listova, žireva i mačica tijekom 2023. i 2024. godine. Sakupljene šiške su secirane i promatrane pod stereomikroskopom analizirajući morfološke karakteristike šiški te ličinke, kukuljice i/ili odrasle osice. Sa 17 zabilježenih vrsta, *Andricus* je najzastupljeniji rod, slijede ga *Neuroterus* s 3 vrste, *Cynips* s 2 vrste i jedna vrsta iz roda *Biorhiza*. Zabilježeno je ukupno 18 oblika šiški, koje su u najvećem broju pronađene na hrastovom pupovima, zatim na listovima i žirevima te na koncu na mačicama cvatova.

Ključne riječi: Cynipidae, ose šiškarice, *Quercus virgiliana*, morfologija šiški

INTRODUCTION

The gall wasps of the family Cynipidae (Hymenoptera: Cynipidae) form the largest group of gall-forming organisms with around 1400 described species worldwide (STONE *et al.*, 2002; STONE & SCHÖNROGGE, 2003; MELIKA & ABRAHAMSON, 2002;

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RONQUIST *et al.*, 2015; BUFFINGTON *et al.*, 2020). They are mainly distributed in the temperate regions of the northern hemisphere, including about 200 described species from Central Europe, 87 species of which have been recorded in Croatia (KWAST, 2012). According to their host plants, morphological characteristics and biology, gall wasps are divided into eight tribes. The Aylacini, with 170 described species, are almost exclusively plant gall wasps, with most species occurring on Asteraceae, Lamiaceae and Rosaceae. The Synergini, with 202 described species, are inquilines (i.e., insects that exploit the living places of another animal) inhabiting the galls of other gall wasps, especially oak gall wasps. The Dipolepidini, with 55 described species, form galls on roses, while the three described species of the tribe Eschatozerini occur exclusively on *Acacia* and *Prosopis* (Fabaceae). Six described species of the tribe Paraulacini are inquilines or parasitoids in chalcidoid galls on *Nothofagus* (Nothofagaceae). The three described species of the tribe Pediaspidini are gallers on *Acer*, while only one species from South Africa belongs to tribe Qwaqwaiini. The tribe that accounts for the majority of cynipid species diversity is Cynipini, and all 1000 described species occur on members of the Fagaceae, mostly on *Quercus* (LILJEBLAD & RONQUIST, 1998; RONQUIST & LILJEBLAD, 2001; LILJEBLAD, 2002; RONQUIST *et al.*, 2015). In Croatia, 68 species of cynipid gall wasps are known to belong to the tribe Cynipini (KWAST, 2012).

Cynipid gall wasps, which are specialized on living oaks of the genus *Quercus*, form a relatively diverse and well-studied community (STONE *et al.*, 2002). In Croatia, cynipid galls have been recorded on the species *Quercus robur* L., *Quercus petraea* (Matt.) Liebl. and *Quercus pubescens* Willd. from the section *Quercus* (subgenus *Quercus*) and on the species *Quercus cerris* L. from the section *Cerris* (subgenus *Cerris*) (KWAST, 2012). The formation of galls on the Virgil oak, also known as the Croatian oak (*Quercus virgiliana* (Ten.) Ten.; syn. *Q. brachyphylloides* Vuk.), has not yet been documented.

The galls of cynipid gall wasps are abnormal growths on all parts of the plant – roots, stems, leaves, axillary and terminal buds, flowers and fruits. The galls form after the female wasp lays her eggs in the plant tissue (RONQUIST *et al.*, 2015). Cynipid gall wasps are important ecological actors that manipulate their host plants to form galls – specialised structures that provide protection and nutrients to developing larvae (WILSON FERNANDES *et al.*, 2012). Most oak gall wasps have a life cycle that involves obligate alternation between a sexual and asexual generation. Many species are currently known from only one of these generations, with the second generation either unknown or described separately under a different name (NICHOLLS *et al.*, 2022).

Structurally, the oak galls of cynipids can be divided into two parts: the larval chamber and the outer gall. The larval chamber, which is structurally similar in all cynipid galls, is lined with nutritious plant tissue on which the larva feeds and is surrounded by a thin wall of sclerenchyma (BRONNER, 1992). The cynipid larva undergoes its entire development in this chamber. The diversity of oak cynipid galls is the result of variations in the gall tissues that develop outside the larval chamber. These include surrounding layers of woody or spongy tissue, complex air spaces within the gall and surface coatings of sticky resins, hairs or spines. Mature galls formed by members of the same genus can also vary greatly in size and color (HARPER *et al.*, 2004). A long-standing challenge in understanding the evolution of gall structure is to explain why such a diversity of morphologies can be found at the same time on the same part of the same host oak species (ASKEW, 1984; PRICE *et al.*, 1987; STONE & COOK, 1998).

Q. virgiliana is a semi-evergreen, hard-leaved tree with low and broad crowns. The distribution area of this species is heterogeneous and includes Corsica, Sardinia, the west coast of the Balkan Peninsula and isolated locations in the Pannonian Plain, on the Black Sea coast of Romania and Bulgaria and on the coasts of the Sea of Marmara and the Aegean (TRINAJSTIĆ, 2007).

The aim of the study is to provide a contribution to the knowledge of gall wasp fauna of Central Dalmatia, including the first report of cynipid galls on the oak species *Q. virgiliana*. We investigated the structure of the community of gall-feeding wasps associated with oaks, focusing on the identification of gall types and their distribution across different plant organs.

MATERIAL AND METHODS

As part of an inspection of the diversity of cynipid gall wasps, galls of *Quercus virgiliana* were examined in a part of the host plant's distribution area in the Lepenica region (Central Dalmatia) (43°37'31.5 "N 16°06'01.6 "E). Samples were collected from 2023 to 2024 in spring and fall. The collection was conducted at three sites, a total of nine trees being sampled, each up to five meters in height, where the presence of galls had been noted during an initial field survey. Each tree served as a fixed sampling point for each collection event. The galls were removed by hand or using manual or telescopic secateurs. The galls and the corresponding plant part were stored separately in labelled bags. During collection, some of the samples were immediately frozen in liquid nitrogen and stored at -80°C for future proteomic and transcriptomic research. The timing of gall collection and the position of galls on the host plants were documented to better understand the phenology of these interactions. Upon arrival at the laboratory, fresh gall samples were dissected and examined under a Leica TL 5000 stereomicroscope to examine larvae, pupae or adult wasps and the galls themselves. Digital images were taken with a Leica DMC 5400 digital camera. The identification of taxa is mainly based on preserved material, but also on additional observations on living larvae, pupae or adult insects. The nomenclature of the species follows ELLIS (2001-2024) and CSÓKA *et al.* (2005). All specimens are deposited in the entomological collections of the Faculty of Science, University of Split, Croatia.

RESULTS

The research identified 17 species of gall-inducing wasps from four genera: *Andricus* (11 species), *Neuroterus* (3 species), *Cynips* (2 species) and *Biorhiza* (1 species). We identified 18 types of galls, with bud galls being the most common and conspicuous, followed by leaf, cupula and catkin galls. Most of the oak galls collected were asexual wasp generations, while bud galls of the sexual generation were recorded only as *Biorhiza* galls, including berry-like galls of *Neuroterus quercusbaccarum* on the male catkins, constituting the eighteenth gall type. We provide illustrated keys for all species, based on their structural and positional diversity, as well as information on the collection period and photographs of larvae, pupae and/or adult cynipids (imago).

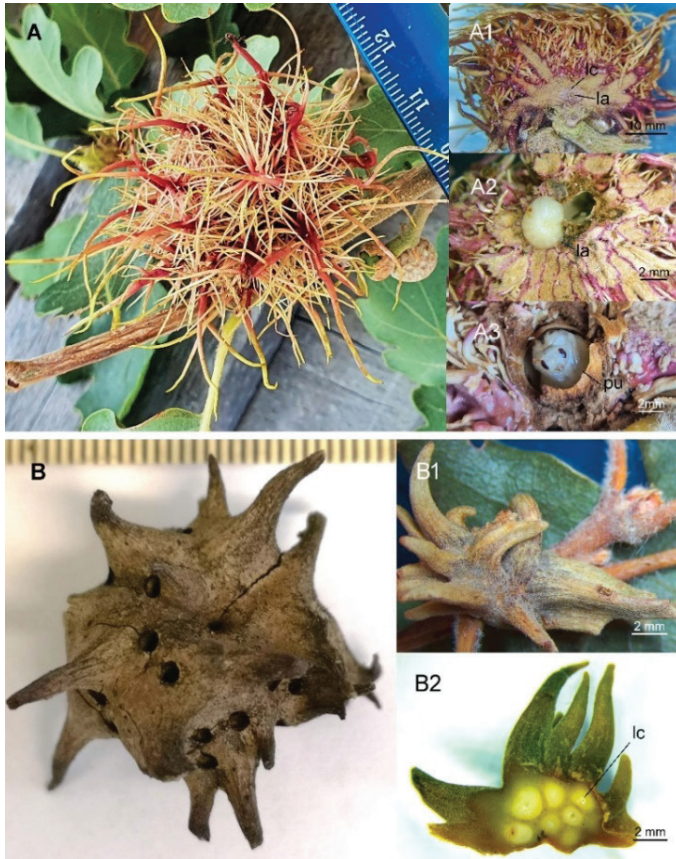


Fig. 1. Galls of cynipid gall wasps: A. *Andricus caputmedusae*; A1. Central longitudinal section through a young gall with single larval chamber (lc) and larva (la); A2. Larva (la); A3. Pupa (pu); B. *Andricus coriarius*; B1. Young gall; B2. Longitudinal section through a multilocular young gall with larval chambers (lc).

Annotated list of species:

Hymenoptera: Cynipidae, Cynipini

***Andricus caputmedusae* (Hartig, 1843)**

Position on the host plant: asexual generation galls (Fig. 1. A, A1, A2, A3) on cupula of *Q. virgiliana*

Collection period: August 2023 (Fig. 1. A2); July 2024 (Fig. 1. A, A1); October 2024 (Fig. 1. A3)

***Andricus coriarius* (Hartig, 1843)**

Position on the host plant: bud galls of the asexual generation (Fig. 1. B, B1, B2) on *Q. virgiliana*

Collection period: July 2024 (Fig. 1. B1, B2)

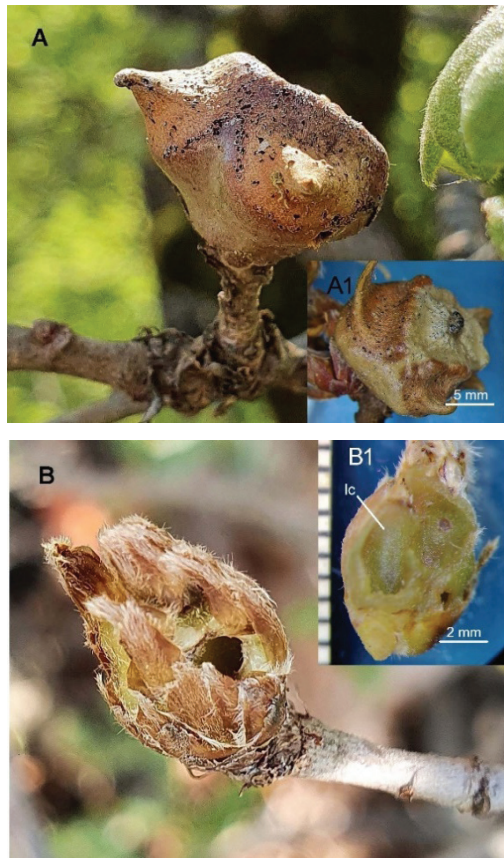


Fig. 2. Galls of cynipid gall wasps: A. and A1 *Andricus coronatus*; B. *Andricus curvator*; B1 Central longitudinal section through a gall with double larval chambers (lc).

***Andricus coronatus* (Giraud, 1859)**

Position on the host plant: bud gall of the asexual generation (Fig. 2. A, A1) develops from an adventitious bud on *Q. virgiliana*

Collection period: July 2024 (Fig. 2. A, A1)

***Andricus curvator* Hartig, 1840**

Position on the host plant: bud gall of the asexual generation (Fig. 2. B, B1) develops from a bud on young shoots of *Q. virgiliana*

Collection period: April 2024 (Fig. 2. B, B1)



Fig. 3. Galls of cynipid gall wasps: A. *Andricus fecundatrix*; A1. Central longitudinal section through a gall with larval chamber (lc) and larva (la); B. *Andricus kollari*; B1 Longitudinal section through a gall with multiple inquiline larval chambers (ilc); B2. *A. kollari* larva (la) and inquiline pupa (ipu); B3. Woody gall with empty inquiline larval chambers (ilc); C. *Andricus malpighii*; D. Woody gall of *Andricus polycerus*

***Andricus fecundatrix* (Hartig, 1840)**

Position on the host plant: bud gall (Fig. 3. A, A1) of the asexual generation on *Q. virgiliana*

Collection period: July 2024 (Fig. 3. A, A1)

***Andricus kollari* (Hartig, 1843)**

Position on the host plant: galls of the asexual generation (Fig. 3. B, B1, B2, B3) develop at the base of a bud of *Q. virgiliana*

Collection period: June 2024 (Fig. 3. B, B3); July 2024 (Fig. 3. B1, B2)

***Andricus malpighii* (Adler, 1881)**

Position on the host plant: bud gall of the asexual generation (Fig. 3. C) develops from an axillary bud of *Q. virgiliana*

Collection period: May 2023 (Fig. 3. C)

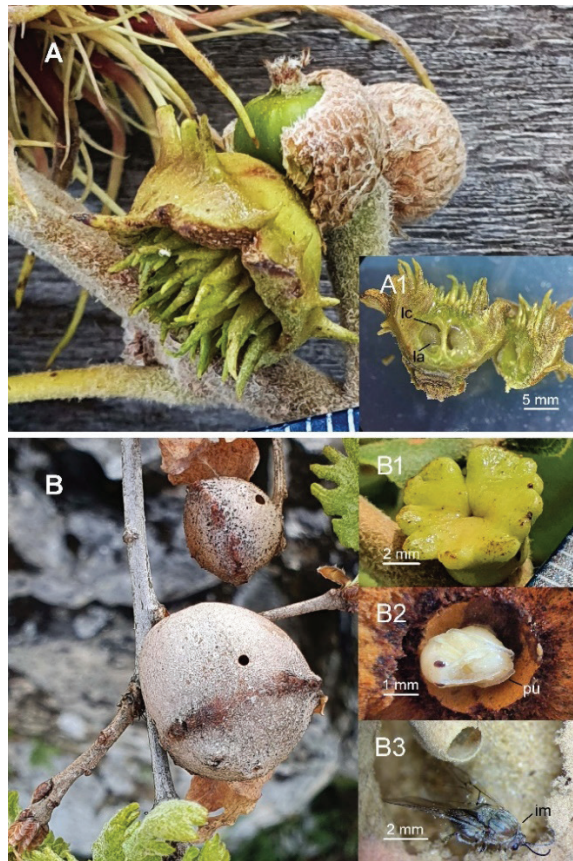


Fig. 4. Galls of cynipid gall wasps: A. *Andricus quercuscalicis*; A1. Longitudinal section through a young gall with double larval chambers (lc) with larva (la); B. *Andricus quercustozae*; B1. Young gall; B2. Longitudinal section through a woody gall with pupa (pu); B3. Longitudinal section through a woody gall with imago (im)

***Andricus polycerus* (Giraud, 1859)**

Position on the host plant: asexual generation bud galls (Fig. 3. D) develop from an adventitious bud on *Q. virgiliana*

Collection period: July 2024 (Fig. 3. D)

***Andricus quercuscalicis* (Burgsdorf, 1783)**

Position on the host plant: asexual generation gall (Fig. 4. A, A1) develops from inside the cupula on *Q. virgiliana*

Collection period: July 2024 (Fig. 4. A, A1)

***Andricus quercustozae* (Bosc d'Antic, 1792)**

Position on the host plant: bud galls of the asexual generation (Fig. 4. B, B1, B2, B3) develop from a bud on a two-year-old shoot of *Q. virgiliana*

Collection period: April 2023 (Fig. 4. B, B3); June 2024 (Fig. 4. B1); October 2024 (Fig. 4. B2)

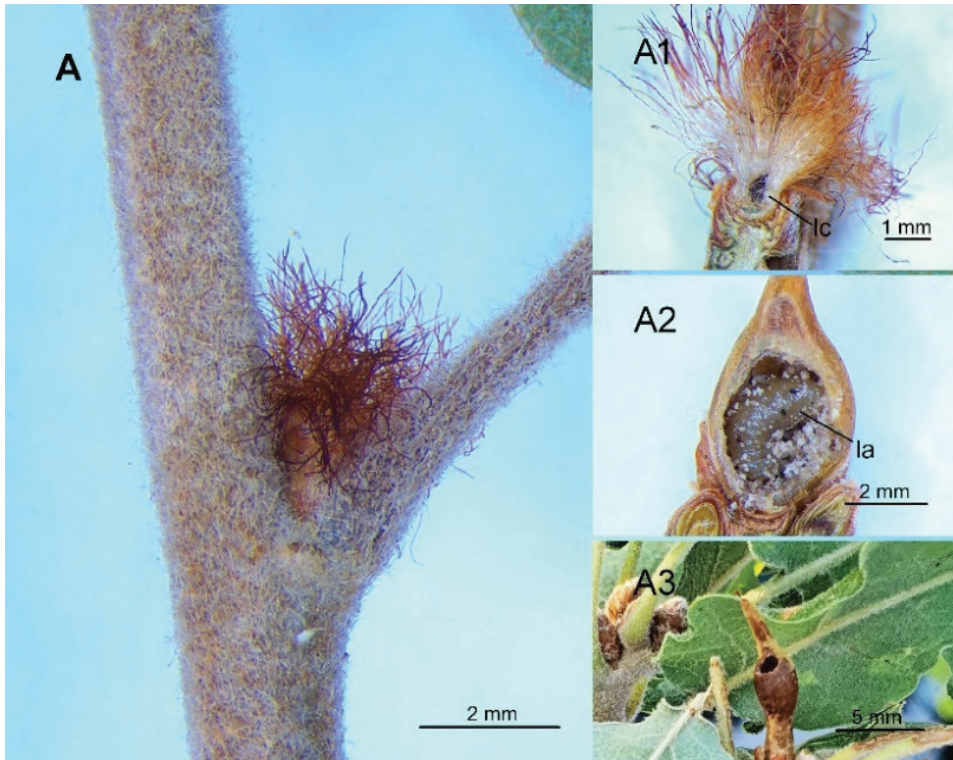


Fig. 5. Galls of cynipid gall wasps: A. *Andricus solitarius*; A1. Longitudinal section through a young gall with visible larval chamber (lc); A1 Longitudinal section through a gall with larva (la); A3. Woody gall with empty larval chambers.

***Andricus solitarius* (Boyer de Fonscolombe, 1832)**

Position on the host plant: bud gall of the asexual generation (Fig. 5. A, A1, A2, A3) develops from an axillary bud of *Q. virgiliana*

Collection period: July 2024 (Fig. 5. A, A1, A2, A3)

***Biorhiza pallida* (Olivier, 1791)**

Position on the host plant: bud gall of the sexual generation (Fig. 6. A, B) on *Q. virgiliana*

Collection period: June 2024 (Fig. 6. A, B)



Fig. 6. Galls of cynipid gall wasps: A. *Biorhiza pallida*; B. Longitudinal section through a gall with visible larvae (la), pupa (pu) and imago (im).

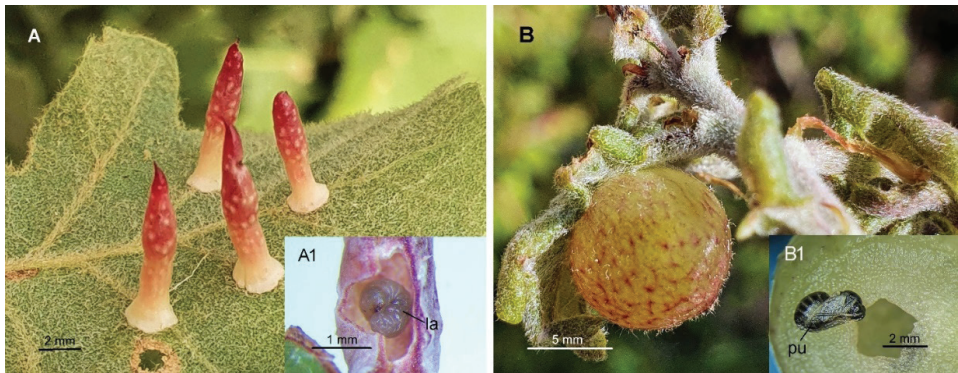


Fig. 7. Galls of cynipid gall wasps: A. *Cynips cornifex*; A1. Longitudinal section through a gall with larva (la); B. *Cynips quercusfolii*; B1. Longitudinal section through a gall with pupa (pu).

***Cynips cornifex* Hartig, 1843**

Position on the host plant: galls of the asexual generation (Fig. 7. A, A1) on the underside of the leaves of *Q. virgiliana*

Collection period: June 2024 (Fig. 7. A, A1)

***Cynips quercusfolii* Linnaeus, 1758**

Position on the host plant: gall of the asexual generation (Fig. 7. B, B1) on the underside of the leaves of *Q. virgiliana*

Collection period: May 2023 (Fig. 7. B, B1)

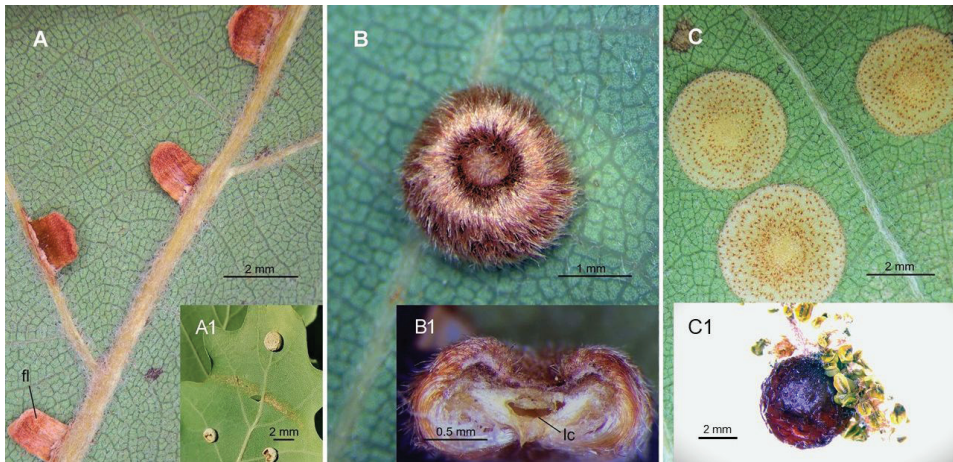


Fig. 8. Galls of cynipid gall wasps: A. *Neuroterus anthracinus*. The flaps (fl) between which the galls will develop; A1. Galls; B. *Neuroterus numismalis*; B1. Longitudinal section through a gall with larval chamber (lc); C. *Neuroterus quercusbaccarum*; C1. Gall of the sexual generation on the male catkin.

***Neuroterus anthracinus* (Curtis, 1838)**

Position on the host plant: the flaps of the asexual generation (Fig. 8. A) on the underside of the leaves of *Q. virgiliana* between which the galls (Fig. 8. A1) will develop

Collection period: July 2024 (Fig. 8. A, A1)

***Neuroterus numismalis* (Geoffroy in Fourcroy, 1785)**

Position on the host plant: galls of the asexual generation (Fig. 8. B, B1) on the underside of the leaves of *Q. virgiliana*

Collection period: July 2024 (Fig. 8. B, B1)

***Neuroterus quercusbaccarum* (Linnaeus, 1758)**

Position on the host plant: galls of the asexual generation (Fig. 8. C, C1) on the underside of the leaves of *Quercus virgiliana*; galls of the sexual generation on the male catkin of *Q. virgiliana* (Fig. 8. C1)

Collection period: July 2024 (Fig. 8. C); June 2024 (Fig. 8. C1)

DISCUSSION

Earlier studies on the species richness of Cynipidae wasps and the morphology of cynipid galls in Croatia were not very extensive (KORLEVIĆ, 1890; MOCSARY, 1897; LANGHOFFER, 1915; JAAP, 1919/20; BAUDYS, 1928, 1941; MEHES, 1939; KWAST, 2012) and did not include species and gall identification on the oak *Quercus virgiliana*. This study constitutes the first documentation of gall-inducing Cynipidae on this oak species in Croatia and expands faunistic knowledge of the interactions between oaks and gall wasps in this region. The identification of 11 *Andricus* species, together with representatives of the genera *Neuroterus*, *Cynips* and *Biorhiza*, emphasizes the significant diversity and taxonomic richness of the gall wasps associated with *Q. virgiliana*.

The contribution of these phytophagous insects to the functional complexity of ecosystems is undisputed (Csóka *et al.*, 2005). Gall wasps play a crucial ecological role in shaping oak communities by generating specialized plant structures (Cuevas-Reyes *et al.*, 2017). The identification of 17 species from four genera and 18 different gall morphotypes reflects a high degree of host specialization and morphological plasticity. The diversity of gall morphologies documented in our study - including bud, leaf, cupula and catkin galls — underlines the ecological adaptability of gall wasps and highlights their ecological and evolutionary importance in colonizing different plant tissues across seasonal phenophases (Stone *et al.*, 2002). These results reflect the adaptive radiation of gall wasps in Mediterranean oak ecosystems, where closely related species have diversified to exploit different ecological niches on the common host (Ronquist & Liljeblad, 2001). This diversification is reflected in the variety of gall morphologies, positions on the plant and seasonal developmental periods observed in association with *Q. virgiliana*. Adaptive radiation in gall-inducing insects, particularly within the family Cynipidae, is a well-documented evolutionary pattern driven by shifts in host tissue preference and phenology rather than host species alone (Stone *et al.*, 2002; Csóka *et al.*, 2005; Ronquist *et al.*, 2015). The phenological synchronization between the life cycles of gall wasps and the developmental stages of their host plants suggests a finely tuned co-adaptive relationship that allows each wasp species to exploit specific developmental windows when plant tissue is most susceptible to gall formation (Stone & Schönrogge, 2003). This phenomenon promotes niche partitioning and reduces interspecific competition between co-occurring species (Bailey *et al.*, 2009).

These findings show *Q. virgiliana* to be a particularly informative system for studying the ecological and evolutionary processes underlying gall formation. Therefore, we suggest that *Q. virgiliana* could serve as a model species for future research on niche diversification, phenological synchronization and the long-term co-evolution of insects and plants in Mediterranean forest ecosystems.

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