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Taxonomy

Confirmation, consequences and causes of extensive polyphyly in the oak gall wasp genus *Dryocosmus* (Hymenoptera: Cynipidae: Cynipini)

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Oak gall wasps are a species-rich group in which most genera induce galls on a single Fagaceae lineage (either a section within *Quercus* or a single non-oak genus). Preliminary data for the few exceptions (most notably *Andricus, Callirhytis, Dryocosmus, and Neuroterus)* suggest that high apparent host plant diversity is an artifact of polyphyly resulting from inadequate morphological definition of genera. Here we demonstrate this issue in *Dryocosmus*, which (as currently defined) galls seven Fagaceae lineages, by reconstructing relationships among 35 species in the genus and 27 other Cynipini genera worldwide. Data for 1,871 base pairs of DNA sequence from 1 mitochondrial gene (cytochrome *b*) and 3 nuclear genes (28S D2, opsin, wingless) confirm that *Dryocosmus* comprises a polyphyletic assemblage of more host-specific lineages. Our analyses also strongly reject monophyly of *Callirhytis*. We surveyed the taxonomic issues underlying these problems in *Dryocosmus* and begin the taxonomic revision of this and closely related genera. We establish (i) *D. asymmetricus* as a junior synonym of *Neuroterus asymmetricus* (Kinsey), **comb. nov.**, (ii) *C. congregata* as a junior synonym of *Melikaiella congregata* (Ashmead), **comb. nov.**, (iii) *C. clavula* as a junior synonym of *Andricus clavula* (Osten Sacken), **comb. rev.**, and (iv) reinstate *Plagiotrochus kunugiphagus* as *Dryocosmus kunugiphagus* Ide & Abe **comb. rev.** We establish a new genus, *Chrysolepicynips* Stone, Nicholls, Melika & Tang, **gen. nov.** for *D. castanopsidis*, *D. demartinii*, *D. juliae and D. rileypokei* that gall chinquapins (*Chrysolepis* sp.). Finally, we identify alternating generations in two species: asexual *C. furva* is a junior synonym of sexual *D. quercusnotha* (Osten Sacken), and asexual *Zopheroteras guttatum* and sexual *D. quercuslaurifoliae* are junior synonyms of sexual *D. quercuspalustris* (Osten Sacken). Our results provide a backbone for revision of *Dryocosmus* and highlight the need for Cynipini-wide revision of polyphyletic genera.

Keywords: host conservatism, host shift, Fagaceae, phylogeny, taxonomy

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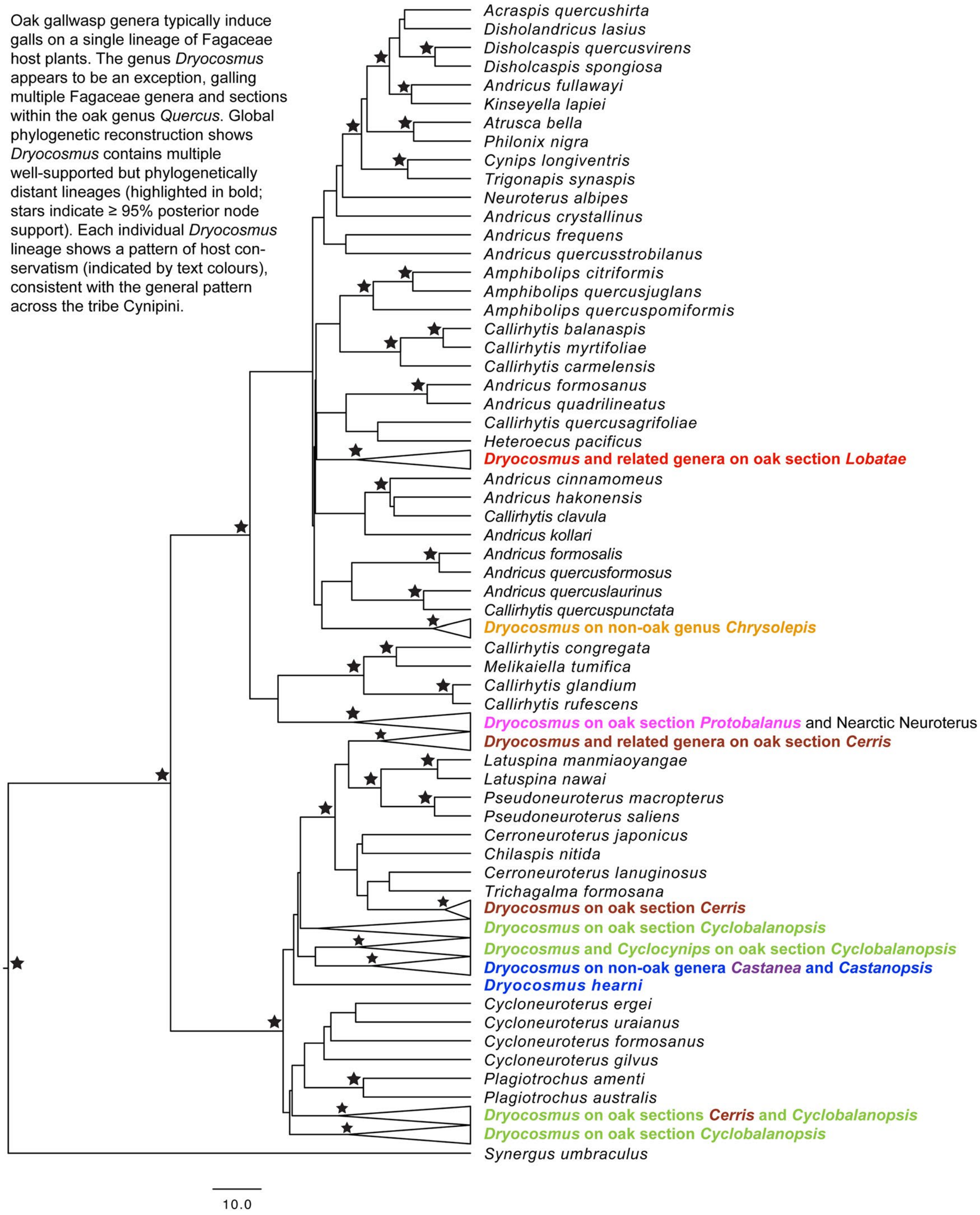
Graphical abstract

Oak gallwasp genera typically induce galls on a single lineage of Fagaceae host plants. The genus *Dryocosmus* appears to be an exception, galling multiple Fagaceae genera and sections within the oak genus *Quercus*. Global phylogenetic reconstruction shows *Dryocosmus* contains multiple well-supported but phylogenetically distant lineages (highlighted in bold; stars indicate ≥ 95% posterior node support). Each individual *Dryocosmus* lineage shows a pattern of host conservatism (indicated by text colours), consistent with the general pattern across the tribe Cynipini.



Introduction

Gall wasps (Hymenoptera: Cynipidae) are endophytophagous insects whose larvae induce and feed on specialized plant tissues, either in *de novo* galls or in galls caused by other insects, on a range of host plant taxa (Csóka et al. 2005). Current gall wasp classification contains 10 tribes (Hearn et al. 2024), each of which is associated with specific host plant lineages. The tribe Cynipini, commonly known as oak gall wasps, is by far the most species-rich, with about 1,000 known species that gall *Quercus* L. and non-oak Fagaceae (Abe et al. 2007, Ronquist et al. 2015, Buffington et al. 2020, Lobato-Vila et al. 2022) (see Table 1 for a summary of geographic distribution and host plant richness in Cynipini genera). With the exception of a clade in each of *Andricus* Hartig and *Callirhytis* Förster (Stone et al. 2009), all Cynipini species are specific to one or more hosts in either a single section (infrageneric monophyletic lineage; Denk et al. 2017, Hipp et al. 2020) of the oak genus *Quercus* (sections *Cyclobalanopsis* Oerst., *Ilex* Loudon, and *Cerris* Dumort. in the subgenus *Cerris*; and sections *Lobatae*

Loudon, *Protobalanus* (Trelease) O. Schwarz, *Quercus sensu stricto*, *Virentes* Loudon, and *Ponticae* Stef. in the subgenus *Quercus*) or a single non-oak genus (*Chrysolepis* Hjelmq. or *Notholithocarpus* Manos, Cannon & S.H.Oh in North America, and *Castanea* Mill., *Castanopsis* (D.Don) Spach, or *Lithocarpus* Blume in Asia) (Burks 1979, Melika 2006, Tavakoli et al. 2021, Lobato-Vila et al. 2022, Ward et al. 2022). A general pattern of host conservatism also exists at the level

Table 1. Summary of geographic distribution and richness of host lineages for global Cynipini genera

Genus	Authority	Geographic distribution	Host plant genera/sections	# of host genera/sections
Acraspis	Mayr, 1881	Nearctic	*Q: Quercus*	1
Amphibolips	Reinhard, 1865	Nearctic	*Q: Lobatae*	1
Andricus	Hartig, 1840	Holarctic, Oriental	*Castanea, Notholithocarpus, Q: Cerris, Q: Lobatae, Q: Ponticae, Q: Protobalanus, Q: Quercus, Q: Virentes*	8
Antron	Kinsey, 1930	Nearctic	*Q: Quercus*	1
Aphelonyx	Mayr, 1881	Western Palaearctic	*Q: Cerris*	1
Atrusca	Kinsey, 1929	Nearctic	*Q: Quercus*	1
Barucynips	Medianero & Nieves-Aldrey, 2013	Nearctic	*Q: Quercus*	1
Bassettia	Ashmead, 1887	Nearctic	*Q: Lobatae, Q: Quercus, Q: Virentes*	3
Belizinella	Kovalev, 1965	Eastern Palaearctic	*Q: Quercus*	1
Belonocnema	Mayr, 1881	Nearctic	*Q: Virentes*	1
Biorhiza	Westwood, 1840	Palaearctic	*Q: Quercus*	1
Burnettweldia	Pujade-Villar, Melika & Nicholls, 2021	Nearctic	*Q: Quercus*	1
Callirhytis	Foerster, 1869	Holarctic	*Q: Cerris, Q: Lobatae, Q: Protobalanus, Q: Quercus, Q: Virentes*	5
Cerroneuroterus	Melika & Pujade-Villar, 2010	Palaearctic, Oriental	*Q: Cerris*	1
Chilaspis	Mayr, 1881	Western Palaearctic	*Q: Cerris*	1
Coffeikokkos	Pujade-Villar & Melika, 2012	Nearctic	*Q: Quercus*	1
Cyclocynips	Melika, Tang, & Sinclair, 2013	Oriental	*Q: Cyclobalanopsis*	1
Cycloneuroterus	Melika & Tang, 2011	Eastern Palaearctic, Oriental	*Castanopsis, Lithocarpus, Q: Cyclobalanopsis*	3
Cynips	Linnaeus, 1758	Western Palaearctic, Nearctic	*Q: Ponticae, Q: Quercus*	2
Disholandricus	Melika, Pujade-Villar & Nicholls, 2021	Nearctic	*Q: Protobalanus*	1
Disholcaspis	Dalla Torre & Kieffer, 1910	Nearctic	*Q: Quercus, Q: Virentes*	2
Dros	Kinsey, 1937	Nearctic	*Q: Quercus*	1
Druon	Kinsey, 1937	Nearctic	*Q: Quercus, Q: Virentes*	2
Dryocosmus	Giraud, 1859	Holarctic, Oriental	*Castanea, Castanopsis, Chrysolepis, Q: Cerris, Q: Cyclobalanopsis, Q: Lobatae, Q: Protobalanus*	7
Erythres	Kinsey, 1937	Nearctic	*Q: Lobatae*	1
Eumayria	Ashmead, 1887	Nearctic	*Q: Lobatae*	1
Eumayriella	Melika & Abrahamson, 1997	Nearctic	*Q: Lobatae*	1
Femuros	Kinsey, 1937	Nearctic	*Q: Quercus*	1
Feron	Kinsey, 1937	Nearctic	*Q: Quercus*	1
Grahamstoneia	Melika & Nicholls, 2021	Nearctic	*Q: Protobalanus*	1
Heteroecus	Kinsey, 1922	Nearctic	*Q: Protobalanus*	1
Heocynips	Fang, Nieves-Aldrey & Melika, 2020	Eastern Palaearctic	*Q: Quercus*	1
Holocynips	Kieffer, 1910	Nearctic	*Q: Lobatae, Q: Protobalanus, Q: Quercus*	3
Kinseyella	Pujade-Villar & Melika, 2010	Nearctic	*Q: Quercus*	1
Kokkocynips	Pujade-Villar & Melik, 2013	Nearctic	*Q: Lobatae*	1
Latuspina	Monzen, 1954	Eastern Palaearctic, Oriental	*Q: Cerris*	1
Loxaulus	Mayr, 1881	Nearctic	*Q: Protobalanus, Q: Quercus, Q: Virentes*	3
Melikaiella	Pujade-Villar, 2014	Nearctic	*Q: Lobatae*	1
Neuroterus	Hartig, 1840	Holarctic	*Lithocarpus, Q: Cerris, Q: Ponticae, Q: Protobalanus, Q: Quercus, Q: Virentes*	6
Neuroandricus	Pujade-Villar & Melika, 2024	Nearctic	*Q: Quercus*	1
Nichollsiella	Melika, Pujade-Villar & Stone, 2021	Nearctic	*Q: Quercus*	1

(Continued)

Table 1. Continued.

Genus	Authority	Geographic distribution	Host plant genera/sections	# of host genera/ sections
Odontocynips	Kieffer, 1910	Nearctic	*Q: Quercus, Q: Virentes*	2
Paracraspis	Weld, 1952	Nearctic	*Q: Protobalanus*	1
Philonix	Fitch, 1859	Nearctic	*Q: Quercus*	1
Phylloteras	Ashmead, 1897	Nearctic	*Q: Quercus*	1
Plagiotrochus	Mayr, 1881	Palaearctic, Oriental	*Q: Cerris, Q: Cyclobalanopsis, Q: Ilex*	3
Prokius	Nieves Aldrey, Medianero & Nicholls, 2021	Nearctic	*Q: Quercus*	1
Protobalandricus	Melika, Nicholls & Stone, 2018	Nearctic	*Q: Protobalanus*	1
Pseudoneuroterus	Kinsey, 1923	Western Palaearctic	*Q: Cerris*	1
Reticulodermis	Pujade-Villar, Cuesta-Porta & Melika, 2024	Nearctic	*Q: Lobatae*	1
Sphaeroteras	Ashmead, 1897	Nearctic	*Q: Quercus*	1
Striatoandricus	Pujade-Villar, 2020	Nearctic	*Q: Quercus*	1
Trichagalma	Mayr, 1907	Eastern Palaearctic, Oriental	*Q: Cerris*	1
Trichoteras	Ashmead, 1897	Nearctic	*Q: Protobalanus*	1
Trigonapsis	Hartig, 1840	Palaearctic	*Q: Quercus*	1
Ussuraspis	Kovalev, 1965	Eastern Palaearctic	*Q: Quercus*	1
Xanthoteras	Ashmead, 1897	Nearctic	*Q: Quercus*	1
Zapatella	Pujade-Villar & Melika, 2012	Nearctic	*Q: Lobatae*	1
Zopheroteras	Ashmead, 1897	Nearctic	*Q: Lobatae, Q: Quercus*	2

Host lineages are listed in alphabetical order for non-oak genera, while sections within the genus *Quercus* start with *Q:* and the section names are listed alphabetically.

of gall wasp genera (Table 1, Supplementary Fig. S1): of 59 recognized genera, 45 induce galls on a single lineage of host Fagaceae. Host conservatism at this host taxonomic level is supported by character state reconstructions showing that while evolutionary shifts among closely related host plant taxa within oak sections have been frequent (Ward et al. 2022), shifts between sections within the genus *Quercus* are very rare (Stone et al. 2009).

Several species-rich and geographically widely distributed gall wasp genera stand out as obvious exceptions to this general pattern of host plant lineage conservatism at the gall wasp genus level (Table 1). The two most notable are *Dryocosmus* Giraud and *Andricus*, which are associated with seven and eight oak sections or non-oak genera, respectively (Table 1, Supplementary Fig. S1). *Andricus* has long been recognized as a poorly defined genus; Kinsey (1922) noted in the 1920s that it was “a meaningless name and does not necessarily express natural relationships of the species thus labelled” and application of this genus name has not improved since (see discussion in Melika et al. 2021a). Because *Andricus* contains many hundreds of species (Melika and Abrahamson 2002), revision of this genus will be a major undertaking, requiring associated taxonomic changes to many other genera across the Cynipini. With 46 described species globally before this study, *Dryocosmus* is a relatively small genus by comparison, yet is still associated with great diversity of host plant genera (4) and a high number of host plant lineages (7 genera or sections within *Quercus*) (Tables 1 and 2). Western Palaearctic *Dryocosmus* species gall oaks in section *Cerris* (Stone et al. 2009, Melika et al. 2010), Nearctic species gall oaks in sections *Lobatae* and *Protobalanus* and the genus *Chrysolepis* (Burks 1979, Buffington and Morita 2009, Nicholls et al. 2018), and Eastern Asian species gall oaks in section *Cyclobalanopsis* and the non-oak genera *Castanea* and *Castanopsis* (Lobato-Vila et al. 2022, Ide et al. 2026).

The high richness of host associations in *Dryocosmus* could indicate the presence of biological traits that facilitate host plant shifts within a monophyletic gall wasp lineage. This is potentially significant for *Dryocosmus* because this genus contains *D. kuriphilus* Yasumatsu, the most economically damaging global pest gall wasp, which is restricted to *Castanea* (Aebi et al. 2006, Abe et al. 2007). Alternatively, high biological diversity in *Dryocosmus* (and in other apparently biodiverse genera, such as *Andricus, Callirhytis*, and *Neuroterus* Hartig; Table 1) may be an artifact caused by the use of taxonomic characters that define a polyphyletic assemblage of biologically divergent lineages, rather than a single natural group. In Cynipini taxonomy, there has been a historical tendency to group morphologically distinct species into relatively small and easily diagnosable genera, while placing less distinctive species into less well-defined “catch-all” genera (sometimes called trashcan or wastebin taxa; Jouault et al. 2022, Reyes-Hernández and Solodovnikov 2024). While trashcan taxa can develop through failure of authors to rigorously apply informative genus-diagnostic traits in new species descriptions (see Discussion), they may also develop through use of diagnostic traits that are poorly defined and/or show extensive convergent evolution. This possibility is suggested by the growing number of studies showing incongruence between phylogenies based on morphology with those based on DNA sequence data, and polyphyly or paraphyly of several large Cynipini genera, including *Andricus*, *Callirhytis*, *Dryocosmus* and *Neuroterus* (Liljeblad et al. 2008, Stone et al. 2009, Nicholls et al. 2017, Nicholls et al. 2018). Such morphological convergence could result from limits on adult morphospace imposed by a galling life history (Ronquist et al. 2015), thus making the identification of genus-level diagnostic characters difficult. The challenge

Table 2. Host associations, geographic distribution, and formally described generations of valid species included in the genus *Dryocosmus* before this study (*D. kunugiphagus* is reinstated in this study), along with a note of nomenclatural changes resulting from this study

Host-plant group	Species	Geographic distribution	Generation	Nomenclatural change
Castanea	* *Dryocosmus kuriphilus* Yasumatsu, 1951	EP	Asexual	No change
	Dryocosmus zhuili Liu & Zhu, 2015	OR	Sexual	No change
Castanopsis	* *Dryocosmus cannoni* Schwéger & Tang, 2016	OR	Sexual	No change
	* *Dryocosmus caputgrusi* Tang & Schwéger, 2016	OR	Sexual	No change
	* *Dryocosmus carlesiae* Tang & Melika, 2011	OR	Sexual	No change
	* *Dryocosmus harrisonae* Melika & Tang, 2016	OR	Sexual	No change
	* *Dryocosmus hearni* Melika & Tang, 2016	OR	Sexual	No change
	Dryocosmus liui Pang, Su & Zhu, 2018	OR	Sexual	No change
	Dryocosmus murakamii Ide & Abe, 2021	EP	Sexual	No change
	* *Dryocosmus pentagonalis* Melika & Tang, 2011	OR	Sexual	No change
	* *Dryocosmus quadripetiolus* Schwéger & Tang, 2016	OR	Sexual	No change
	* *Dryocosmus testisimilis* Tang & Melika, 2011	OR	Sexual	No change
	* *Dryocosmus triangularis* Melika & Tang, 2011	OR	Sexual	No change
Chrysolepis	* *Dryocosmus castanopsidis* (Beutenmueller, 1917)	NA	Asexual	Moved to *Chrysolepicynips* gen. nov.
	* *Dryocosmus demartinii* Melika, Nicholls & Stone, 2018	NA	Asexual	Moved to *Chrysolepicynips* gen. nov
	* *Dryocosmus juliae* Melika, Nicholls & Stone, 2018	NA	Sexual	Moved to *Chrysolepicynips* gen. nov
	* *Dryocosmus rileypokei* Morita & Buffington, 2009	NA	Sexual Asexual	Moved to *Chrysolepicynips* gen. nov
Quercus* subgenus *Cerris* section *Cerris	* *Dryocosmus caspiensis* Melika, Sadeghi, Atkinson, Stone & Barimani, 2008	WP	Asexual	No change
	* *Dryocosmus cerriphilus* Giraud, 1859	WP	Sexual Asexual	No change
	* *Dryocomus destefanii* Cerasa & Melika, 2018	WP	Sexual Asexual	No change
	* *Dryocosmus jungalii* Melika & Stone, 2010	WP	Sexual	No change
	* *Dryocosmus kunugiphagus* Ide anbd Abe 2015	EP OR	Sexual Asexual	Reinstated from the genus *Plagiotrochus*
	* *Dryocosmus mayri* Müllner, 1901	WP	Sexual	No change
	* *Dryocosmus mikoi* Melika, Tavakoli, Stone & Azizkhani, 2006	WP	Sexual	No change
	* *Dryocosmus tavakolii* Melika, Stone & Azizkhani, 2006	WP	Sexual?	No change
Quercus* subgenus *Cerris* section *Cyclobalanopsis	* *Dryocosmus crinitus* Schwéger & Tang, 2016	OR	Asexual	No change
	* *Dryocosmus hualieni* Schwéger & Tang, 2016	OR	Asexual	No change
	* *Dryocosmus konradi* Tang & Melika, 2016	OR	Sexual	No change
	* *Dryocosmus liyingi* Melika & Tang, 2016	OR	Sexual	No change
	* *Dryocosmus moriius* Tang & Melika, 2016	OR	Sexual	No change
	Dryocosmus sakureiensis Ide, Wachi & Abe, 2013	EP	Sexual	No change
	* *Dryocosmus salicinai* Schwéger & Tang, 2016	OR	Sexual	No change
	Dryocosmus sefuriensis Ide, Wachi & Abe, 2013	EP	Sexual	No change
	* *Dryocosmus taitungensis* Tang & Melika, 2016	OR	Asexual	No change

(Continued)

Table 2. Continued.

Host-plant group	Species	Geographic distribution	Generation	Nomenclatural change
Quercus subgenus *Quercus* section *Lobatae*	* *Dryocosmus albidus* Weld, 1944	NA	Asexual	No change
	Dryocosmus archboldi Melika & Abrahamson, 2021	NA	Sexual	No change
	Dryocosmus cinereae (Ashmead, 1887)	NA	Sexual	No change
	* *Dryocosmus dubiosus* (Fullaway, 1911)	NA	Sexual Asexual	No change
	Dryocosmus favus Beutenmueller, 1911	NA	Asexual	No change
	Dryocosmus floridensis (Beutenmueller, 1917)	NA	Sexual	No change
	* *Dryocosmus minusculus* Weld, 1952	NA	Asexual	No change
	* *Dryocosmus quercuslaurifoliae* (Ashmead, 1881)	NA	Sexual	Junior synonym of *D. quercuspalustris*
	* *Dryocosmus quercusnotha* (Osten Sacken, 1870)	NA	Sexual	Senior synonym of *C. furva*
	* *Dryocosmus quercuspalustris* (Osten Sacken, 1861)	NA	Sexual	Senior synonym of *D. quercuslaurifoliae* and *Z. guttatum*
Quercus subgenus *Quercus* section *Protobalanus*	* *Dryocosmus asymmetricus* (Kinsey, 1922)	NA	Asexual	Junior synonym of *N. asymmetricus*
Host unknown	*Dryocosmus nanlingensis* Abe, Ide, & Odagiri, 2014	OR	Sexual	No change
	Dryocosmus okajimai Abe, Ide, Konishi & Ueno, 2014	OR	To be determined	No change

Species sampled in this study are marked with an asterisk (*). Host plant information was drawn from Weld (1957, 1959, 1960), Burks (1979), Pénzes et al. (2018), Roskam (2019), and Lobato-Vila et al. (2022). Metadata of sampled species are in Supplementary Table S1. Abbreviations for geographic distribution are: EP, Eastern Palaearctic; NA, Nearctic; OR, Oriental Region; WP, Western Palaearctic.

facing Cynipini taxonomy is illustrated by the fact that the sexual and asexual generation adults that make up the cyclically parthenogenetic life cycles of most Cynipini (Stone et al. 2002) have sometimes been allocated to different genera (Lyon 1970, this study). Whatever the cause, since genera are the means by which species-level information is organized, grouping of unrelated and potentially biologically diverse species in polyphyletic taxa is an impediment to further study and understanding. Correcting this situation requires confirmation of the phylogenetic status of genera and, where poly- or paraphyletic, the identification of morphological characters that define new monophyletic taxa.

To place these taxonomic issues in *Dryocosmus* in context, we first describe the morphological characters used to define the genus. The genus *Dryocosmus* was established in 1859 (Giraud 1859), based on the designation of the type species *D. cerriphilus* Giraud, a European species associated with *Quercus* section *Cerris*. Current diagnostic characters of *Dryocosmus* mostly follow Weld (1952b), who provided a fundamental taxonomic revision of worldwide Cynipoidea as then understood, with further elaboration in Melika et al. (2010). By defining what was at that time a monotypic genus, Giraud may potentially have confounded species-level characters with genus-level characters for *Dryocosmus*. Subsequent revisions have resulted in the definition of *Dryocosmus* by a particular combination of character states for a large suite of characters, some of which share potentially plesiomorphic states with other genera. The main characters currently used can be summarized as follows. The head of *Dryocosmus* species is broader than high in frontal view (Fig. 1A), nearly 2.0× as broad as long in dorsal view (Fig. 1C). The head is smooth, alutaceous to delicately coriaceous, without setae, and with striae radiating from the clypeus. The gena is broadened behind the eye (asexual female) or not (sexual generation) (Fig. 1A and B). There is no malar sulcus, with a very short malar space (Fig. 1A). The number of flagellomeres varies within and between generations. In the sexual generation, the antenna has 12–13 flagellomeres in females and 13 in males. Male antennal segment F1 is excavated and clearly expanded apically. In the asexual female, the antenna has 11–12 flagellomeres. The mesosoma is convex and nearly as high as long in lateral view, with very few white setae (Fig. 1D). The mesoscutum is smooth or alutaceous (Fig. 1E). The notauli are complete and deeply impressed; the median mesoscutal line is absent or in the form of a very short triangle; anterior parallel and parapsidal lines are absent (Fig. 1E). The mesoscutellum is smooth or uniformly coriaceous (Fig. 1F). Scutellar foveae are absent or present, usually presenting as an anterior transverse impression (Fig. 1F), which is indistinctly delimited posteriorly from the mesoscutellar disk. Sometimes a narrow, weak central carina extends to the mesoscutum, dividing the anterior impressed area into 2. The mesopleuron and speculum are uniformly alutaceous or smooth (Fig. 1D). The lateral propodeal carinae bend outwards medially (Fig. 1G); the median longitudinal carina is present or absent,

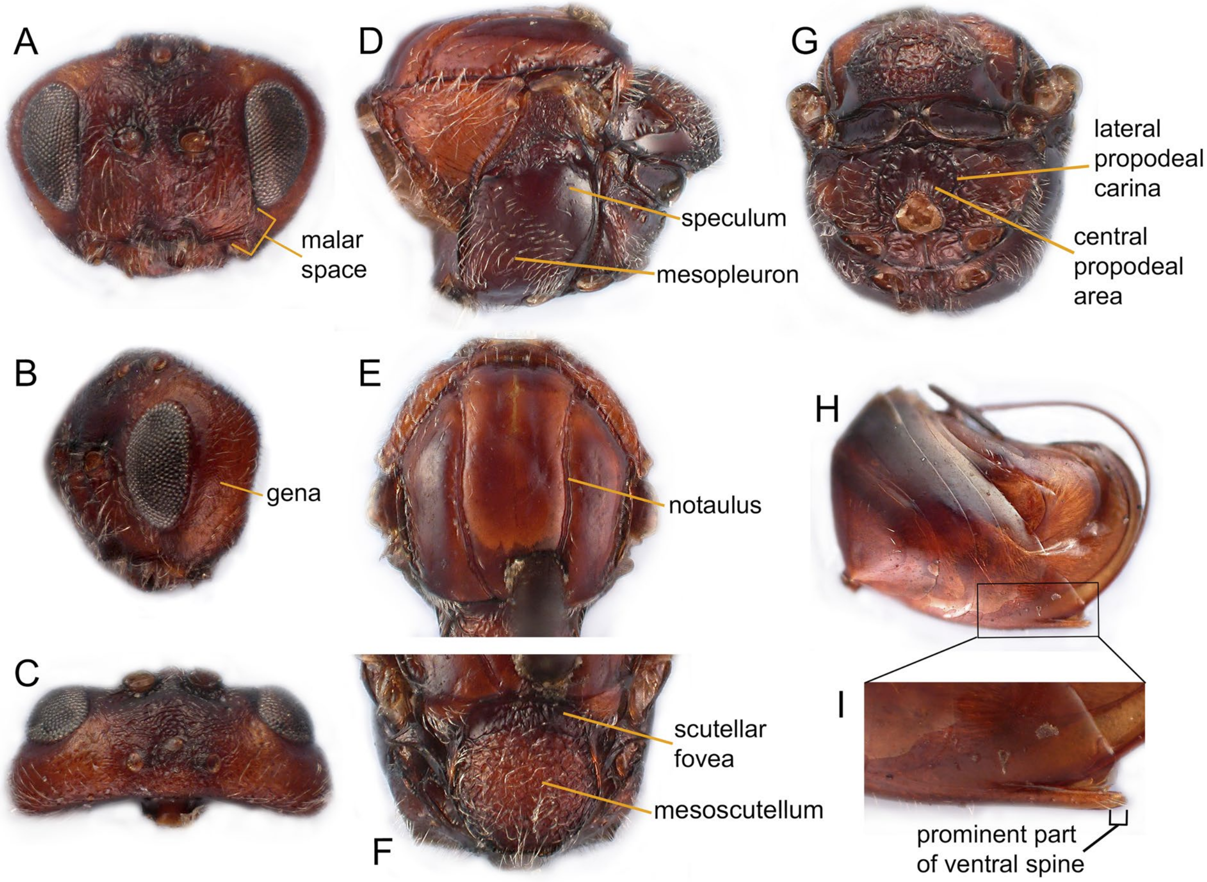


Fig. 1. Morphological characters of the type species of *Dryocosmus*, *Dryocosmus cerriphilus* Giraud, asexual female. A–C) head: A, frontal view; B, lateral view; C, dorsal view. D–G) mesosoma: D, lateral view; E, mesoscutum, dorsal view; F, mesoscutellum, dorsal view; G, posterior view. H) metasoma, lateral view. I) prominent part of ventral spine, lateral view. Morphological terms mentioned in the main text are indicated.

and irregular wrinkles are present in the central propodeal area (Fig. 1G). The tarsal claws are simple, without basal lobes. The radial cell of the forewing is open and 3.5–4.0× as long as broad. The metasoma is compressed laterally, as long as it is high and higher than the mesosoma (Fig. 1H). All terga have no setae or punctures (except for the metasoma in *D. kuriphilus*, which has uniform dense micropunctures except on the second metasomal tergum). The prominent part of the ventral spine of the hypopygium is short, with short and sparse setae, which never present as an apical tuft (Fig. 1I).

There has long been a feeling among Cynipini taxonomists that application of these morphological characters has resulted in a non-monophyletic set of *Dryocosmus* species (Melika and Abrahamson 2002, Ács et al. 2007, Melika et al. 2011). An early molecular phylogenetic analysis by Ács et al. (2007) rejected *Dryocosmus* monophyly, but was limited both by the taxon sampling (only 5 Western Palaearctic, 1 Oriental and 1 Nearctic *Dryocosmus* species) and the number of independently evolving sequence markers used (1 nuclear locus and 2 linked mitochondrial loci). The most recent molecular analysis of *Dryocosmus* (Nicholls et al. 2018) had more extensive sampling (14 Nearctic and 2 Palaearctic species, although 4 of the Nearctic species have subsequently been transferred to *Kokkocynips* Pujade-Villar and Melika (Nieves-Aldrey et al. 2021)) but had very limited sampling of east Asian and Oriental taxa and was based on a single mitochondrial locus. Recent molecular studies of Cynipini using much larger numbers of loci (eg, Ward et al. 2022) have supported non-monophyly of *Dryocosmus*, but (given that this was not the intended focus) included too few *Dryocosmus* species to allow focused reassessment of the genus.

Here we use DNA sequence data from four unlinked loci (1 mitochondrial and 3 nuclear) to assess the monophyly of *Dryocosmus* and hence to distinguish between the 2 possible explanations for the observed high host plant richness of the genus. If *Dryocosmus* as currently defined is monophyletic, then the high host plant richness is genuine. In contrast, if *Dryocosmus* is a polyphyletic amalgamation of non-sister lineages, then this genus and its associated high host plant diversity are artifacts of poor gall wasp taxonomy. In this case, new morphological synapomorphies will be required to define each component monophyletic lineage within *Dryocosmus* for reallocation of species to new genera reflecting natural groups. Our dataset includes sequence data for 35 *Dryocosmus* species, spanning the known global distribution of the genus and including 74% of the currently recognized species richness. We infer the relationships among these taxa and representatives of 27 other Cynipini genera, for a total of 104 species, using the 4-gene phylogeny. In the light of our results, we consider the shortcomings of the taxonomic characters currently used to define *Dryocosmus*, propose some initial taxonomic revisions (including the pairing of currently separated sexual and asexual generation taxa), and highlight the need for a Cynipini-wide revision of *Dryocosmus* and other problematic genera.

Materials and Methods

Species Sampling

Dryocosmus species were reared from galls collected across the Holarctic and Oriental regions between 2007 and 2019 (Figs 2 and 3). Metadata for all specimens are provided in Supplementary Table S1. In some cases, noted in Supplementary Table S1, larvae were dissected from galls identified to species and gall generation (sexual or asexual generation in the cyclical parthenogenetic gall wasp lifecycle) on the basis of diagnostic host-plant associations and gall morphologies. All other samples were adults whose initial identification based on gall characters was subsequently verified using adult morphology. All specimens were preserved in 99% ethanol after emergence or gall dissection.

We sampled 35 *Dryocosmus* species, including 7 from the Western Palaearctic, 17 from the Eastern Palaearctic and Oriental regions, and 11 from the Nearctic. These taxa include all except one of the known host plant lineage associations at the oak section and non-oak genus level recorded for the genus (Table 2). The exception is the oak section *Quercus sensu stricto*, which is the host for only one unsampled *Dryocosmus* species—the doubtfully placed Japanese species *D. squamus* (Monzen) (Pénzes et al. 2018). To allow assessment of *Dryocosmus* monophyly, our sampling included members of 27 additional gall wasp genera spanning Cynipini phylogenetic diversity (including multiple lineages in other putatively problematic genera, *Andricus, Callirhytis*, and *Neuroterus*), resulting in 104 species in total (Supplementary Table S1). The oak gall inquiline *Synergus umbraculus* (Olivier) (Hymenoptera: Cynipidae: Synergini) was used as an outgroup (Nicholls et al. 2018). All specimens were sampled in compliance with local permitting requirements (see Supplementary Table S1).

Sequence Generation

We attempted to amplify 4 gene fragments for all study species, comprising fragments of the mitochondrial locus cytochrome *b* (cytb, 433 base pairs, bp) and 3 nuclear loci: the D2 region of the 28S ribosomal RNA nuclear gene (D2, ~562 bp), long-wavelength opsin (opsin, ~500 bp), and wingless (377 bp). In addition to previously published sequences, we generated new sequences for 29 species for cytb, 61 species for D2, 67 species for opsin, and 78 species for wingless (Supplementary Table S1). Full details of DNA extractions, primers used for DNA amplification, and PCR conditions are described in Supplementary Files S1 and S2 and Supplementary Table S2. All new sequences are deposited in GenBank, with accession numbers listed in the data availability statement and Supplementary Table S1. Alignments for each locus were constructed in MAFFT online version 7 with the G-INS-i iterative refinement method (Katoh et al. 2019). All cytb and wingless sequences were 433 bp and 377 bp long, respectively, and could be aligned unambiguously. The D2 sequences had variable length and resulted initially in an alignment of 581 bp. We edited this alignment to exclude regions that were difficult to align unambiguously, resulting in a final alignment of 562 bp. The opsin sequence amplified by primers opsinF and opsinR contains an intron and initially generated a 745 bp long alignment. We edited the alignment to 499 bp by excluding the long insertions present in the intron for *Cycloneuroterus ergei* Tang and Melika and the outgroup *S. umbraculus* and some sites in the intron that were difficult to align unambiguously. All protein-coding gene sequences were translated into amino acids using AliView (Larsson 2014), and no stop codons (as typically associated with nuclear pseudogenes of mitochondrial genes; Rokas et al. 2003b) were detected. The original alignments, edited alignments, and phylogenies generated in this paper are deposited in the Edinburgh DataShare Repository (https://doi.org/10.7488/ds/7902).

Substitution Model Selection and Phylogenetic Analyses

Full details of our model selection approach are provided in Supplementary File S3, and selected models are summarized in Supplementary Table S4. The partitioning scheme was hierarchical by gene and within each gene by codon positions. The non-coding intronic region of opsin and the 28S D2 region were each treated as single partitions. Codon positions showing similar levels and types of sequence variation were further combined into the same partition (for details of each gene, see Supplementary File S3 and Supplementary Table S3). A suitable substitution model for each partition was identified in jModelTest 2 v0.1.10 using the Bayesian Information Criterion (BIC) (Darriba et al. 2012).

We examined the phylogenetic information content and saturation of each partition by plotting the uncorrected pairwise p-distance against inferred branch-length distances among taxa following Klopfstein et al. (2013) and Malm and Nyman (2015). The script utilizing the ape package (Paradis et al. 2004) in R (RStudio Team 2021) was provided by Klopfstein et al. (2013). Branch-length distances were obtained from a ML tree inferred in IQ-TREE 2.1.2 (Minh et al. 2020) using the full concatenated dataset of 1,871 bp with a RAxML-style partition file outlining the simplified partitioning described above and applying an independent GTR+F substitution model to each partition. The script was revised to allow automatic matching of taxon names between the input tree and sequences of each partition and exporting of a .csv file of both pairwise uncorrected p-distance and distance on the tree (available at: https://github.com/TermCIC/dist.calculation/blob/main/dist.calculation.r). This analysis showed a positive correlation between the two distances with no (most partitions) or limited (cytb3) evidence of reaching an asymptote (Supplementary Fig. S2), indicating minimal saturation, so we therefore included all partitions in further phylogenetic analyses.

We performed phylogenetic analyses using both Bayesian and maximum likelihood approaches. Our Bayesian approach inferred 4-locus species trees using the StarBEAST2 module (Ogilvie et al. 2017) implemented in BEAST v2.6.4 (Bouckaert et al. 2019). The appropriate substitution models were simplified to those available in StarBEAST2 (see Supplementary File S3, Supplementary Table S4). Tree topologies and clock models were linked for different codon positions within a gene. Gene ploidy was set to 2.0 for nuclear genes and 0.5 for the mitochondrial cytb. We specified a constant size population model and a birth-death model tree prior. We employed nested sampling (NS) (Skilling 2006, Maturana et al. 2019) to determine which clock model (strict clock or

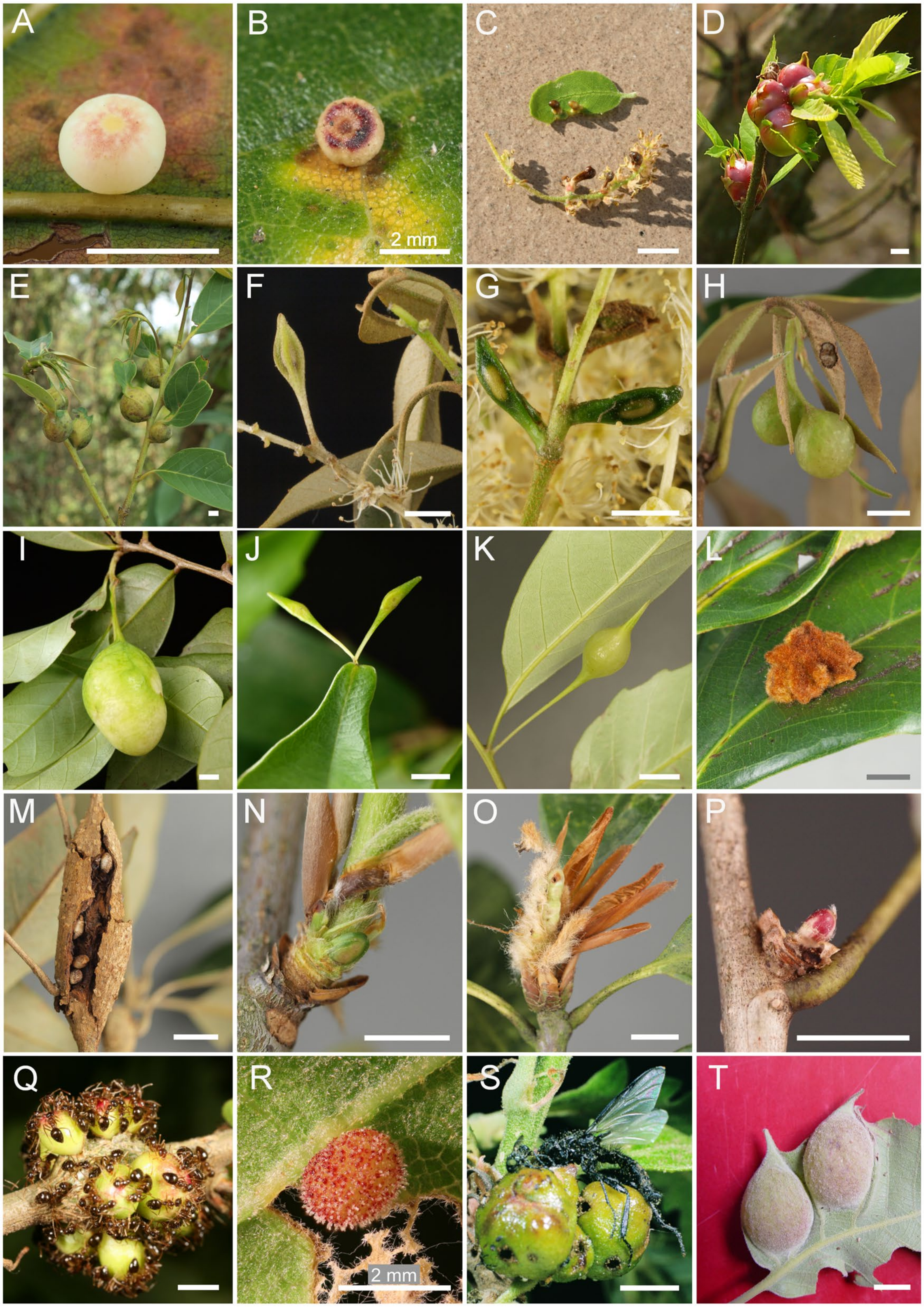


Fig. 2. Examples of galls of *Dryocosmus* species examined in this study. A) *D. albidus*, asexual gall on *Quercus rubra* (subgenus *Quercus*, section *Lobatae*). B) *D. minusculus*, asexual gall on *Q. agrifolia* (subgenus *Quercus*, section *Lobatae*). C) *D. dubiosus*, sexual galls on *Q. agrifolia*. D) *D. kuriphilus*, asexual galls on *Castanea mollisima*. E) *D. hearni* sexual galls on *Castanopsis* sp. F) *D. pentagonalis*, sexual gall on *Castanopsis carlesii*. G) *D. triangularis*, sexual galls on *Castanopsis carlesii*. H) *D. carlesiae*, sexual galls on *Castanopsis carlesii*. I) *D. testisimilis*, sexual gall on *Castanopsis uraiana*. J) *D. caputgrusi*, sexual galls on *Castanopsis uraiana*. K) *D. cannoni*, sexual gall on *Castanopsis echinocarpa*. L) *D. crinitus*, asexual galls on *Q. sessilifolia* (subgenus *Cerris*, section *Cyclobalanopsis*). M) *D. taitungensis* asexual galls on *Q. hypophaea* (subgenus *Cerris*, section *Cyclobalanopsis*). N) *D. moriius*, sexual galls on *Q. morii* (subgenus *Cerris*, section *Cyclobalanopsis*). O) *D. liyingi*, sexual galls on *Q. morii*. P) *D. salicinai*, sexual gall on *Q. salicina* (subgenus *Cerris*, section *Cyclobalanopsis*). Q) *D. cerriphilus* asexual galls on *Q. cerris* (subgenus *Cerris*, section *Cerris*). R) *D. destefanii*, sexual galls on *Q. suber* (subgenus *Cerris*, section *Cerris*; image courtesy of Salvatore Sottile). S) *D. mayri*, sexual galls on *Q. cerris* (image courtesy of György Csóka). T) *D. mikoi*, sexual galls on *Q. brantii* (subgenus *Cerris*, section *Cerris*). All scale bars are 5 mm unless otherwise noted.

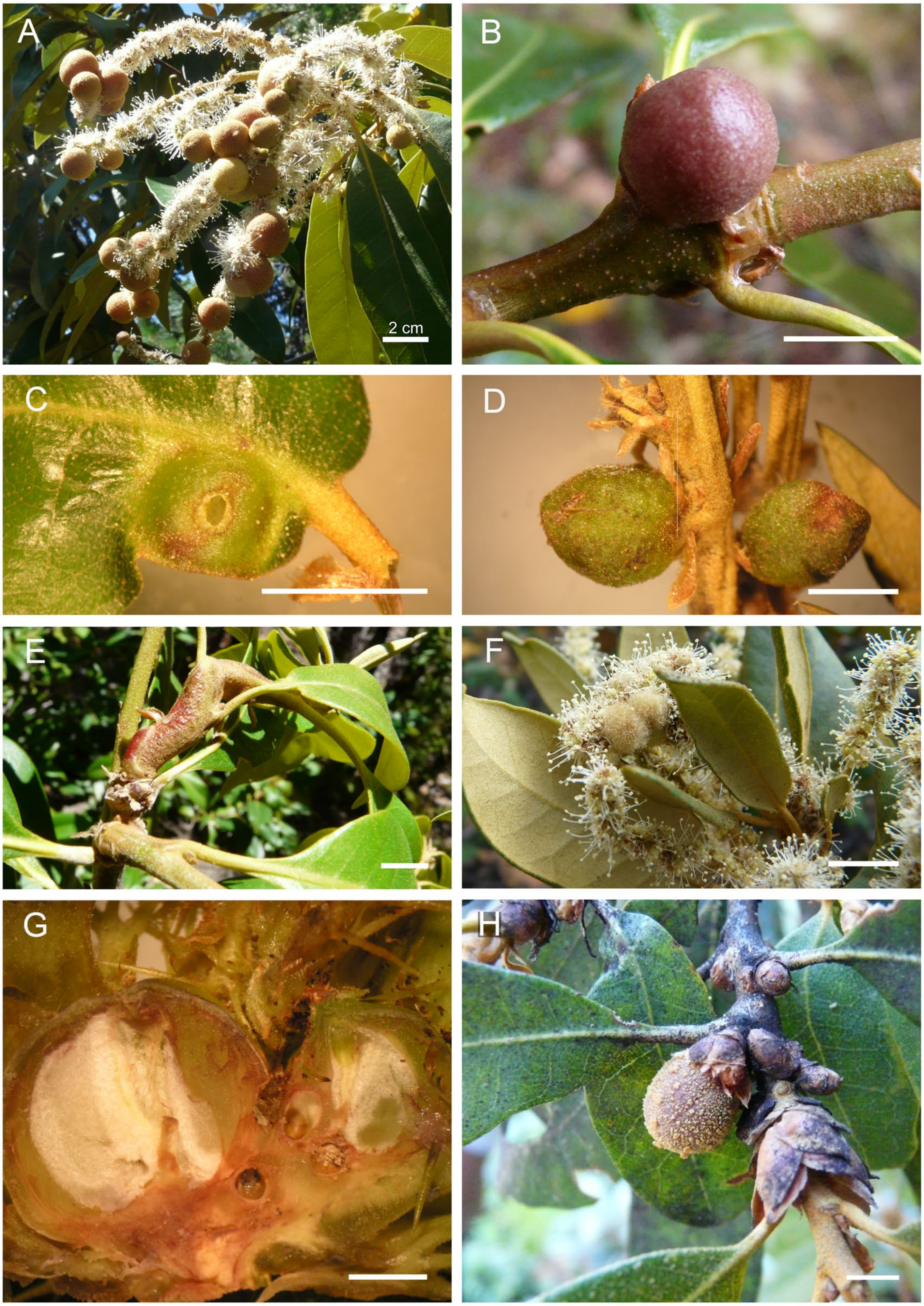


Fig. 3. Galls of *Chrysolepicynips* species associated with *Chrysolepis* host plant species. A) *Chrysolepicynips castanopsidis*, asexual generation galls on catkins. B) *C. demartinii*, asexual generation gall on a bud. C–E) *D. juliae*, sexual generation galls: C, integral leaf gall; D, galls on developing leaf buds; E, integral shoot gall. F) *C. juliae*, asexual generation galls on catkins. G–H) *C. rileypokei*: G, dissected developing fruit showing larval cells inside; H, asexual generation gall in bud. All scale bars are 5 mm unless otherwise noted.

uncorrelated lognormal) was more suitable for the data, following the instructions in the "Taming the BEAST" tutorial (Barido-Sottani et al. 2018, https://taming-the-beast.org/tutorials/NS-tutorial/). Runs for both clock models used the following parameter settings: chainLength = 1,000,000, particleCount = 5, and subChainLength = 100,000. The difference in the log of marginal likelihoods between models was used to calculate Bayes Factors (BF) following Kass and Raftery (1995). BF overwhelmingly

Table 3. Results of nested sampling analyses to select the best clock model for species tree inference and test support for the monophyly of the genera *Dryocosmus* and *Callirhytis*

Model	N	H	SD	Marginal likelihood	BF	2 * √(SD1^2+SD2^2)	Model selection result
Uncorrelated lognormal clock	5	884.53	13.40 (SD1)	−25971.35	134.99	38.51	BF > 2 * √(SD1^2 + SD2^2) uncorrelated lognormal clock is overwhelmingly supported
Strict clock	5	942.07	13.83 (SD2)	−26106.34			
without *Dryocosmus* monophyly	5	884.53	13.40 (SD1)	−25971.35	646.41	41.05	BF > 2 * √ (SD1^2+SD2^2) non-monophyly of *Dryocosmus* is overwhelmingly supported
with *Dryocosmus* monophyly	5	1230.10	15.55 (SD2)	−26617.76			
without *Callirhytis* monophyly	5	884.53	13.40 (SD1)	−25971.35	440.23	42.23	BF > 2*√ (SD1^2+SD2^2) non-monophyly of *Callirhytis* is overwhelmingly supported
with *Callirhytis* monophyly	5	1376.80	16.32 (SD2)	−26411.58			

N is the number of particles and H is the information.

supported the uncorrelated lognormal clock (Table 3), which was used in all subsequent analyses. Our final StarBEAST analyses used two independent runs of 100 million generations, each sampled every 10,000 generations. Convergence of parameters was confirmed by visualization in Tracer 1.7.2 (Rambaut et al. 2018). The last 20 million generations were sampled to estimate the maximum clade credibility species tree in TreeAnnotator, a package included in BEAST v2.6.4., with common ancestor height specified for the node height. The tree file was edited in FigTree v1.4.4 (https://github.com/rambaut/figtree/releases).

We carried out a maximum likelihood analysis using the concatenated four-gene data matrix in IQ-TREE 2.1.2 (Minh et al. 2020). The partitioning scheme was the same as in the analyses in StarBEAST2. Node support was obtained by performing a Shimodaira-Hasegawa approximate likelihood-ratio test (SH-aLRT, Guindon et al. 2010) with 1000 bootstrap replicates using the "-alrt" flag and 1,000 ultrafast bootstrap replicates (UFBoots2, Hoang et al. 2018) using the "-bb" flag, each of which used nearest neighbor interchange (NNI) using the "-bnni" flag to optimize the respective bootstrap tree. We also ran a standard bootstrap (BS) analysis using the same partitioning scheme with 1,000 replicates and NNI to optimize trees in IQ-TREE 2.1.2. Nodes were considered reliable with support values of SH-aLRT ≥ 80 and UFBoots2≥95 following the manual of IQ-TREE, and BS ≥ 80 following Zaharias et al. (2023). The output tree file was edited in FigTree v1.4.4.

Testing *Dryocosmus* and *Callirhytis* Monophyly

To test the hypothesis that *Dryocosmus* is not a monophyletic group, we used BF to compare support for alternative phylogenetic models with and without a constraint of *Dryocosmus* monophyly. *Dryocosmus* monophyly was imposed when setting up the input .xml file in BEAUti prior to running in StarBEAST2 (https://www.beast2.org/constraints-of-monophyly). We used the same approach to test the monophyly of *Callirhytis*, as this genus was also recovered as polyphyletic, with constituent species often intermingled with *Dryocosmus* species. Our sampling for this genus (14 of approximately 115 species globally) was less comprehensive than for *Dryocosmus*, but we consider our results still informative about the status of monophyly of this genus.

Additional Sequencing for Generation Matching

To confirm probable matching of alternate sexual and asexual generations, we sequenced the cytb and the nuclear ITS2 regions for additional individuals in 2 groups of species: *D. quercusnotha* (Osten Sacken)/*Callirhytis furva* Weld, and *D. quercuslaurifoliae/(Ashmead) D. quercuspalustris* (Osten Sacken)/*Zopheroteras guttatum* Weld (see 5.4. Generation matching in *Dryocosmus*). These 2 loci have been used successfully in DNA barcoding-based allocation of oak gall wasp individuals to species, and the combination avoids erroneous grouping of samples based on sharing of mitochondrial sequences through introgression (eg, Nicholls et al. 2018, Cuesta-Porta et al. 2022, Nicholls et al. 2022, Cuesta-Porta et al. 2023). All specimens of *C. furva*, *D. quercusnotha*, *D. quercuspalustris*, and 4 *Z. guttatum* were collected from the original host plant species *Q. palustris* Münchh. (WFO 2025). We sequenced 6 individuals of *D. quercusnotha* and 5 individuals of *C. furva* for cytb, and 4 of the 6 *D. quercusnotha* individuals and the same 5 individuals of *C. furva* for ITS2. From the other group of species, we sequenced a total of 25 individuals for cytb (8 individuals of *D. quercuslaurifoliae*; 6 individuals of *D. quercuspalustris*; 7 and 4 individuals of *Z. guttatum* from *Q. phellos* L. and *Q. palustris*, respectively). Of these we sequenced ITS2 in a subset of 15 individuals (4 individuals of *D. quercuslaurifoliae*; 3 individuals of *D. quercuspalustris*; 4 individuals of *Z. guttatum* from *Q. phellos* and 4 individuals of *Z. guttatum* from *Q. palustris*). PCR conditions for ITS2 followed Campbell et al. (1993), with the same sequencing approach for both loci as used to generate the 4-gene dataset. The protein coding cytb sequences were translated into amino acids, and no stop codons were detected using AliView (Larsson 2014). New sequences for this generation matching have been deposited in Genbank with accession numbers listed in the data availability statement and Supplementary Table S5.

Taxonomic Revision

For taxonomic revisions, we followed Liljeblad et al. (2008), Melika (2006) and Melika et al. (2010) for terminology of gall wasp morphology. For abbreviation of forewing venation, we followed Ronquist and Nordlander (1989).

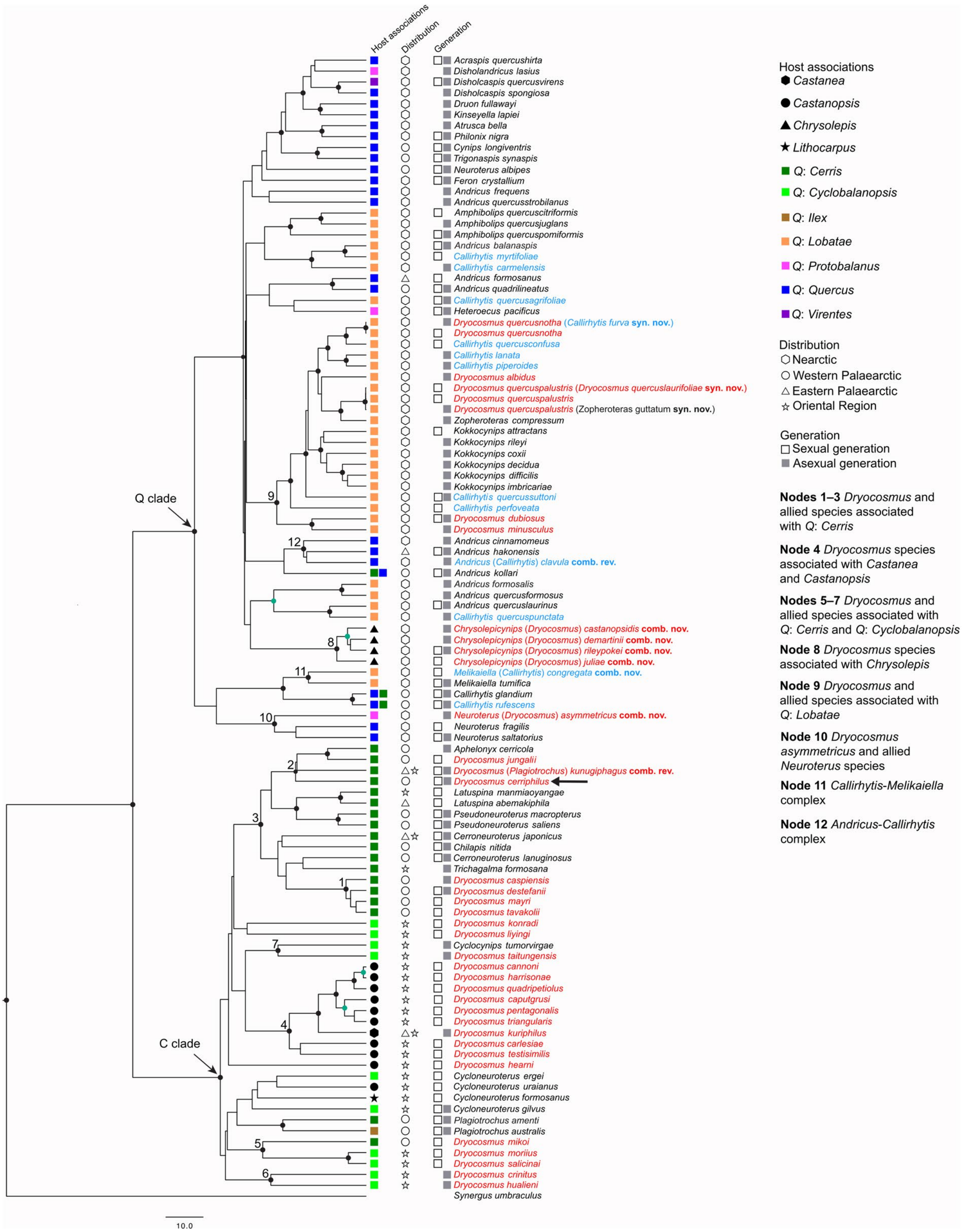


Fig. 4. Maximum clade credibility tree from a four-gene species tree analysis estimated in StarBEAST2. Species coloured in red were all included in *Dryocosmus* before this study (with the type species *D. cerriphilus* indicated by a black arrow), and species in light blue were in *Callirhytis*, indicating the polyphyletic nature of both genera. *Dryocosmus kunugiphagus* is reinstated from the genus *Plagiotrochus* in this study. Numbered and lettered nodes correspond to nodes mentioned in the main text. Host plant associations, species distribution and known generations are annotated by different filled or outlined shapes; host associations with different sections within *Quercus* are annotated by different colours of square. All nomenclatural changes presented in this study are indicated in the phylogeny. Black circles indicate nodes having posterior probability ≥ 0.95, blue-green circles indicate nodes with posterior probability 0.90–0.94, while nodes without dots have support < 0.90.

Results

Phylogenetic Overview

The phylogenies resulting from the StarBEAST and ML analyses showed very similar topologies and recovered the same host-specific lineages in *Dryocosmus*. Each host-specific lineage shows strong monophyly in both the StarBEAST analysis with posterior probability (PP) ≥ 0.95 (Fig. 4) and in the ML analyses with UFBoot ≥ 95 and SH-aLRT ≥ 80, and BS ≥ 80 (Supplementary Fig. S3). The StarBEAST and ML phylogenies differ only in the relative placement of a few species in other genera at poorly supported nodes along the backbone of the tree (Fig. 4, Supplementary Fig. S3). Phylogenies for each of the component loci (Supplementary Figs S4–S7) supported similar topologies, including strong support for the fundamental division of Cynipini into 2 monophyletic clades (PP ≥ 0.95): one associated with host plants in the oak subgenus *Cerris* and the non-oak Fagaceae genera *Castanea*, *Castanopsis*, and *Lithocarpus* (referred to hereafter as the C clade), and a second clade associated with oaks in the subgenus *Quercus* and the non-oak genus *Chrysolepis* (referred to hereafter as the Q clade) (Fig. 4, Supplementary Fig. S3). We therefore regard this set of loci as capturing a strong phylogenetic signal and providing a stable basis for assessment of taxon monophyly. Below we use the maximum clade credibility tree (Fig. 4) to describe the groupings of *Dryocosmus*.

Dryocosmus Is Polyphyletic

Dryocosmus species are distributed across both of the major C and Q clades, each of which contains both multispecies groups of *Dryocosmus* and isolated species that are most closely related to (or nested among) members of other genera. This clearly shows that, as currently circumscribed, *Dryocosmus* is polyphyletic. Unsurprisingly given this distribution, the BF comparison of models with and without the constraint of *Dryocosmus* monophyly strongly rejected monophyly (Table 3).

An unexpected outcome of our sequencing, indicative of the taxonomic challenges in Cynipini, was the pairing of sexual generations of *Dryocosmus* with asexual generations currently placed in other genera. Firstly, sequences obtained for sexual generation adults of *D. quercusnotha* are almost identical to those obtained for asexual generation *C. furva*. Secondly, sequences obtained for sexual generation adults of *D. quercuslaurifoliae* and *D. quercuspalustris* are almost identical to sequences for asexual *Z. guttatum*. These results, supported by additional sequence data from more individuals, are discussed in a formal taxonomic framework below.

We now summarize the phylogenetic distribution of *Dryocosmus* species associated with each oak section or non-oak genus. We navigate through the phylogeny using numbered nodes with high support (PP ≥ 0.95) in Fig. 4.

In the C clade:

i. *Quercus* section *Cerris*. *Dryocosmus* species galling this oak section are widely distributed through the C clade. Four *Dryocosmus* species on *Cerris* oaks form a monophyletic lineage (node 1). Two others, *D. cerriphilus* and *D. jungalii* Melika and Stone, are in a paraphyletic assemblage, including *Aphelonyx cerricola* (Giraud) and *Plagiotrochus kunugiphagus* (Ide and Abe) (node 2). Nodes 1 and 2 both fall within a larger clade in which all species gall section *Cerris* oaks (node 3). Finally, *D. mikoi* Melika, Tavakoli, Stone and Azizkhani is the only section *Cerris*-associated species in a clade more often associated with *Quercus* section *Cyclobalanopsis* (node 5).
ii. *Quercus* section *Cyclobalanopsis*. *Dryocosmus* species galling this oak section are also widely distributed through the C clade. *Dryocosmus konradi* Tang & Melika and *D. liyingi* Melika and Tang are isolated taxa. *Dryocosmus moriius* Tang & Melika and *D. salicinai* Schwéger and Tang are a strongly supported pairing that is sister to *D. mikoi* (node 5), while *D. crinitus* Schwéger and Tang and *D. haulieni* Schwéger and Tang form another strongly supported pairing (node 6), possibly allied to the *Dryocosmus* taxa of node 5. *Dryocosmus taitungensis* Tang & Melika is sister to *Cyclocynips tumorvirgae* Melika and Tang (node 7), which also galls section *Cyclobalanopsis* oaks.
iii. *Castanopsis* and *Castanea*. All but one of the *Dryocosmus* species that gall *Castanopsis* form a clade that additionally includes the chestnut gall wasp *D. kuriphilus* on *Castanea* (node 4). The exception, *D. hearni* Melika and Tang, is in an unresolved and phylogenetically distant position outside this clade.

In the Q clade:

i. *Chrysolepis*. *Dryocosmus* species galling the chinquapins form a monophyletic lineage (node 8) that is distant from all other *Dryocosmus* species and is clearly phylogenetically distinct on a relatively long branch within the Q clade.
ii. *Quercus* section *Lobatae*. *Dryocosmus* species galling red oaks form a paraphyletic assemblage (node 9) that also includes species in *Callirhytis*, *Kokkocynips* (species of which were previously placed in *Dryocosmus*), and *Zopheroteras* Ashmead. The affinity of *Dryocosmus* and *Zopheroteras* is also reflected in a recent analysis based on ultraconserved elements (UCEs) (Ward et al. 2022).
iii. *Quercus* section *Protobalanus*. The only *Dryocosmus* species on intermediate oaks, *D. asymmetricus* (Kinsey), is distant from all other *Dryocosmus* species and is sister to two Nearctic *Neuroterus* species (*N. saltarius* Weld and *N. fragilis* Bassett) that gall section *Quercus* oaks (node 10).

Callirhytis Is Polyphyletic

Our analysis also shows *Callirhytis* to be polyphyletic (Fig. 4). BF comparison of models with and without the constraint of *Callirhytis* monophyly strongly rejects monophyly for this genus (Table 3). In contrast to *Dryocosmus*, *Callirhytis* species are restricted only to the Q clade, although they clearly do not form a natural group. Instead, different *Callirhytis* species are allied to *Andricus*, *Dryocosmus*, *Kokkocynips*, *Melikaiella* Pujade-Villar, and *Zopheroteras* species. Polyphyly is also apparent for *Andricus* and *Neuroterus*, although we do not formally test their non-monophyly due to our sparse sampling of these genera.

High Richness of Host Associations of *Dryocosmus* Is a Taxonomic Artefact

Our analysis shows that the wide host plant range of *Dryocosmus* is an artifact of its polyphyletic status. Most currently recognized *Dryocosmus* species in our analysis belong to one of four well-supported monophyletic clades, each of which shows strongly conserved host plant associations with one of *Chrysolepis* (Fig. 4, node 8), *Castanopsis* (Fig. 4, node 4, with the exception of *D. kuriphilus* on *Castanea*), section *Cerris* oaks (Fig. 4, node 3), or section *Lobatae* oaks (Fig. 4, node 9), although in the latter two cases *Dryocosmus* species are intermingled with species from other genera. Hence, if the nomenclature of *Dryocosmus* species is ignored, they conform to the existing paradigm of gall wasp lineage-level specialization to a single oak section or genus of non-oak Fagaceae.

Discussion

Polyphyly of *Dryocosmus*

This study encompassed comprehensive global sampling of *Dryocosmus* and geographically and phylogenetically diverse sampling of 27 other Cynipini genera associated with five host plant genera within the Fagaceae. We showed that *Dryocosmus* as currently defined morphologically is polyphyletic and in need of major revision, reinforcing previous studies (Ács et al. 2007, Stone et al. 2009, Blaimer et al. 2020, Ward et al. 2022). *Dryocosmus* is divided among four major, but distantly related, lineages (2 in the Q clade [nodes 8 and 9] and 2 in the C clade [nodes 1 and 4]) and multiple isolated taxa, one of which is *D. cerriphilus*, the type species for the genus. Each of the main *Dryocosmus* lineages has a narrow host plant range at the oak section or non-oak genus level, showing high biological diversity in this genus to be an artefact of polyphyly and reinforcing the general pattern of host plant conservatism in Cynipini.

Although not the focus of this study, we also formally confirmed the non-monophyly of *Callirhytis* and illustrate non-monophyly in *Andricus* and *Neuroterus*. Our findings agree with previous studies (Liljeblad et al. 2008, Stone et al. 2009, Nicholls et al. 2017) and underline the taxon polyphyly problem for both taxonomic and evolutionary studies of the Cynipini. Because species in all 4 of these problematic genera are intermingled in the Cynipini phylogeny and are currently defined by non-exclusive sets of morphological traits (see below), they all need to be revised within a Cynipini-wide context that incorporates extensive taxon sampling. In what follows we focus on *Dryocosmus* and closely allied genera.

Causes of Morphological Chaos in *Dryocosmus*

Misapplication of Diagnostic Traits

Some of the trouble with *Dryocosmus* stems from inconsistent application in new species descriptions of genus-level diagnostic criteria, which mostly follow Weld (1952b). In both sexual and asexual generation *Dryocosmus*, Weld (1952b) defined diagnostic dimensions for the prominent part of the ventral spine (ppvs) as "ventral spine at most two and a half times as long as broad in side view," and defined the mesopleuron as smooth or polished. This combination is true for the *Dryocosmus* type species *D. cerriphilus* (a European species that galls *Quercus cerris*). However, both characters have not been rigorously applied simultaneously in some species descriptions. For example, the mesopleuron in the asexual generation female of *D. albidus* Weld (Weld 1944) is largely bare and coriaceous with a few faint striae (not smooth or polished as required), and the ppvs is 8 times as long as broad in side view (and not 2.5×, as required). In asexual generation female *D. minusculus* Weld, the mesopleuron is bare and smooth, but the ppvs is also 8 times as long as broad in side view (Weld 1952a). This type of misapplication is also found in some *Castanopsis*-galling *Dryocosmus* species. While the dimensions of the ppvs in this lineage match Weld's original definition, the presence of transverse striated markings on the mesopleuron (Melika et al. 2011, Tang et al. 2016) does not follow the smooth or polished character state required for *Dryocosmus*. Such misapplication is not restricted to *Dryocosmus*; Melika and Abrahamson (2002) highlight the fact that only a small proportion of Nearctic *Callirhytis* species show the primary diagnostic character of this genus (a transversely sculptured scutum) proposed in its original description. Similar misapplication of diagnostic traits may explain the long-recognized non-monophyly of *Andricus* and perhaps also *Neuroterus* (Melika and Abrahamson 2002, Stone et al. 2009).

Use of Ambiguous Traits in Generic Definitions

Another problem is the use of ambiguous characters in the original diagnosis of genera and resulting ambiguity in diagnostic keys. For example, a character used to separate *Callirhytis* and *Dryocosmus* in modern generic keys concerns sculpture on the mesopleuron (Melika and Abrahamson 2002, Melika 2006). However, the original generic descriptions described similar mesosomal sculpturing patterns in both genera (eg, Beutenmuller 1911, Weld 1944, 1952a). Furthermore, the key in Weld (1952b) gives a smooth mesoscutum as the diagnostic character for both *Dryocosmus* and *Callirhytis* section B. This results in ambiguous generic placement of some taxa (see Lyon 1970) and may have resulted in arbitrary placement of species in one or the other genus. Part of this problem has been addressed by improved keys (Melika and Abrahamson 2002) and the recent transfer of some *Dryocosmus* and *Callirhytis* species into the newly created genera *Kokkocynips*, *Melikaiella*, and *Zapatella* Pujade-Villar and Melika (Pujade-Villar et al. 2012, 2014, Nieves-Aldrey et al. 2021). However, examination of specimens used in this study showed that species with asexual *Kokkocynips*-like mesopleural sculpturing remain in both *Dryocosmus* (eg, asexual female of *Dryocosmus albidus*) and *Callirhytis* (asexual females of *C. furva*, *C. lanata* [Gillette], and *C. piperoides* [Bassett]). This suggests that additional revision of phylogenetically validated diagnostic characters remains an important task when defining natural groupings of species in *Dryocosmus, Callirhytis*, and related genera.

Ambiguity in the naming of morphological structures may also have contributed to a confused taxonomy of Cynipini species (see Melika and Abrahamson 2000). Melika and Abrahamson (2000) provide a set of morphological characters that have been used in the past to separate genera but have since been shown to vary among species within multiple genera and even between individuals of the same species, adding further confusion to generic limits. Given the apparent limited morphological variation among Cynipini taxa, most genera in Cynipini are by necessity circumscribed based on possessing a combination of character states (see, for example, recent descriptions of novel or reinstated genera; Melika et al. 2021b, Cuesta-Porta et al. 2022, 2023). Liljeblad et al. (2008) provided a set of morphological characters that defined the tribe Cynipini but then stated that in many cases they had secondary reversals or modifications to more plesiomorphic states in specific Cynipini lineages. Hence there is a very real chance that the combination of characters used to define genera such as *Dryocosmus* includes some plesiomorphic character states, facilitating the inclusion of multiple unrelated lineages in a single genus and highlighting the challenge facing taxonomic revision of Cynipini genera into natural monophyletic groups.

Conflicting Taxonomies of Sexual and Asexual Generations

Cyclical parthenogenesis is characteristic of almost all Cynipini species, and galls, gall locations, and adult morphologies are distinct in the two generations (Stone et al. 2002). The 2 generations of many species have been paired experimentally, and both experimental and DNA barcoding approaches continue to be used for this purpose (eg, Pujade-Villar et al. 2001, Rokas et al. 2003b, Ács et al. 2007, Stone et al. 2008, Ide et al. 2010, Wachi and Abe 2010, Melika et al. 2013, Ide and Abe 2015, 2016, 2019, Cerasa et al. 2020). An interesting feature of our phylogenetic analysis is that sequence data sometimes pair a sexual generation taxon in one genus with an asexual generation taxon in another genus. This is apparent in the clade of red oak-associated gall wasps defined by node 9 in Fig. 4, in which some sexual generation *Dryocosmus* are paired with asexual generation *Callirhytis* and *Zopheroteras*. This issue may stem from the structure of the key in Weld (1952b) in which available diagnostic characters can only be applied to sexual—but not asexual—generation specimens. Hence the sexual *Dryocosmus* associated with red oaks (*Quercus* section *Lobatae*; *D. quercusnotha*, *D. quercuslaurifoliae*, and *D. quercuspalustris*) run to a different part of the key than their relevant asexual forms (which key out as *Zopheroteras* or *Callirhytis* species). Other examples of this problem have been reported in other studies (for example, Lyon 1970, Cuesta-Porta et al. 2023), and taken together these findings reinforce the fact that taxonomic revision of *Dryocosmus* (or any other Cynipini genus) requires careful reassessment of diagnostic characters for both sexual and asexual generations.

The Status of *Cerris*-Galling *Dryocosmus* and Allied Genera

The *Dryocosmus* species galling section *Cerris* oaks (including the type species *D. cerriphilus*) represent a non-monophyletic group within the clade defined by node 3 in Fig. 4, with a 4-species lineage in 1 part of the clade (node 1) and 2 species in a separate subclade (node 2) allied to *Aphelonyx* Mayr and *P. kunugiphagus*. This provides further evidence for the failure of genus-level circumscription. The close phylogenetic affinity of *D. cerriphilus* with *Aphelonyx* implies that revision of *Dryocosmus* requires concurrent treatment of *Aphelonyx*, and if clear morphological characters were to be found that reliably group species within the clade defined by node 2, then potentially *Aphelonyx* would become a junior synonym of *Dryocosmus*.

The Status of *Castanopsis*- and *Castanea*-Galling *Dryocosmus*

Node 4 of our phylogeny in Fig. 4 recovered strong support for the monophyly of most *Castanopsis*-galling *Dryocosmus* species and the global *Castanea*-galling pest *D. kuriphilus*. *Dryocosmus kuriphilus* reproduces parthenogenetically, while other members in the same lineage are only known from their sexual generation (although males of *D. caputgrusi* Tang and Schwéger and *D. quadripetiolus* Schwéger and Tang have not yet been discovered). Sexual reproduction is also known in the chestnut-galling species *D. zhuili* Liu & Zhu (not present in our sampling), which galls *Castanea henryi* (Lu et al. 2012, Zhu et al. 2015). *Dryocosmus zhuili* was distinguished from *D. kuriphilus* based on 2.3% sequence divergence for the mitochondrial COI gene (Lu et al. 2012). While this level of divergence in DNA barcode data is often considered to indicate separate species status (Hebert et al. 2003), it also falls within the range of population-level divergence of some widespread Western Palaearctic gall wasp species (Rokas et al. 2003a, Nicholls et al. 2012). *Dryocosmus kuriphilus* is a widespread species in China (Lu et al. 2012, Liu et al. 2024), and it is possible that *D. zhuili* represents a sexually reproducing lineage within a wider *D. kuriphilus*/*zhuili* species complex.

Nevertheless, the current analysis clearly shows that the *Dryocosmus* species on *Castanea* are closely related to those galling *Castanopsis*. The transverse striated markings on the mesopleuron of sexual *D. zhuili* (sometimes also faintly present in *D. kuriphilus*; Zhu et al. 2015) could be homologous to the transverse striated markings on the mesopleuron of sexual generation *Castanopsis*-galling *Dryocosmus* species (Melika et al. 2011, Tang et al. 2016). Hence, the discovery of the currently unknown asexual generations for taxa grouped in node 4 is necessary for comparison with the asexual-only species *D. kuriphilus* before any robust genus-level taxonomic re-characterization of this lineage can be done.

The Status of *Cyclobalanopsis*-Galling *Dryocosmus*

Our phylogeny revealed *Dryocosmus* species galling section *Cyclobalanopsis* oaks to have arisen from the poorly resolved base of the C clade. While this was not an aim of our study, low support for critical basal nodes means that our data cannot discriminate between *Cyclobalanopsis* as an ancestral host for the C clade with multiple subsequent transitions to other hosts or multiple parallel evolutions of a *Cyclobalanopsis* host association. Inference of ancestral host plant associations will require a larger set of loci (eg, based on ultraconserved elements [UCEs]; Zhang et al. 2019, Blaimer et al. 2020) and additional sampling of Cynipini associated with endemic Asian Fagaceae host plant taxa.

Generation Matching of *D. quercuspalustris*

Our results indicate that *D. quercuspalustris* is the sexual generation of the asexual species *Z. guttatum*, with identical or near-identical cytb and ITS2 sequences between the 2 species. This result is in apparent conflict with the UCE-based phylogenetic analysis of Ward et al. (2022) (their Supplementary Figs S2–S5 and S7–S9), in which the asexual generation species *Z. sphaerula* Weld was nested within a clade of 5 sexual generation samples of *D. quercuspalustris*. That *Z. sphaerula* and *Z. guttatum* are distinct asexual generation species is supported by Weld's (1952a) morphological diagnosis between them and the distinct differences in their galls, as well as clear differences in their oak host associations (Weld 1959). Despite being described 100 years ago, *Z. sphaerula* has only been recorded from *Q. rubra* L., while *Z. guttatum* is known from a range of section *Lobatae* hosts: *Q. buckleyi* Dorr and Nixon, *Q. coccinea* Münchh., *Q. palustris*, *Q. imbricaria* Michx., *Q. phellos*, and *Q. texana* Buckley (Weld 1959, our sampling; *Q. rubra* is also likely to be a host for *Z. guttatum*—see https://bugguide.net/node/view/579097#body). *Dryocosmus quercuspalustris* has a similarly broad range of host plant species; Weld 1959 explicitly listed it occurring on 10 host species, but also noted it was found on all red oaks (Weld 1959, p. 111).

A likely explanation for this situation could be the existence of (at least) 2 cryptic species whose sexual generations induce identical *D. quercuspalustris* gall morphotypes, with 1 species having a broad host range of section *Lobatae* species and inducing a *Z. guttatum*-type asexual gall, and the other being much more host specific and inducing a *Z. sphaerula*-type asexual gall. This situation whereby there is a lack of morphological distinction between sexual generation galls of closely related species has been previously reported for several other Cynipini groups (Abe et al. 2021, Sottile et al. 2025). Our sampling incorporates the host plant of the *D. quercuspalustris* and *Z. guttatum* type specimens; hence, we have likely sequenced the cryptic taxon within this complex that the name *D. quercuspalustris* correctly applies to. We suggest that Ward et al. (2022) sampled another cryptic species from *Q. rubra*, which has *Z. sphaerula* as its alternate generation. Further sampling using genetic data with better species-level resolution than UCEs would be needed to test among these explanations.

Gall Morphological Diversity as an Indicator of Non-Monophyly in *Dryocosmus*

Gall morphology is very diverse across *Dryocosmus* sensu lato. Most Cynipini genera established using molecular and adult morphological data show relatively conserved host plant associations and, to a varying degree, conserved gall locations and morphology (Cook et al. 2002, Ward et al. 2022). Specific examples include Nearctic genera *Disholcaspis* (Nicholls et al. 2017), *Druon* (Cuesta-Porta et al. 2022), and *Feron* (Cuesta-Porta et al. 2023). While gall morphology is quite strongly conserved in some lineages (such as Western Palaearctic *Cynips* and Nearctic *Atrusca* [Bailey et al. 2009, Cuesta-Porta et al. 2025]), it is much more variable in other lineages, such as *Kokkocynips* (Nieves-Aldrey et al. 2021) and *Disholandricus* (Melika et al. 2021b), and host-alternating *Andricus* in the Western Palaearctic (Bailey et al. 2009). From this perspective, the very high morphological diversity in *Dryocosmus* sensu lato (Figs 2 and 4) is consistent with (although not proof of) polyphyletic status (as demonstrated in Fig. 4). Some specific lineages within *Dryocosmus* sensu lato show more conserved morphology, for example, *Dryocosmus* on *Castanopsis* (Fig. 2E–K), implying that revision of *Dryocosmus* into a new set of genera is likely to reduce intrageneric gall diversity substantially. However, the new genus *Chrysolepicynips*, which we establish below for *Dryocosmus* species galling *Chrysolepis*, shows that even a small clade of closely related species can show high gall diversity in both generations (Fig. 3).

Taxonomic Treatments

Here we provide some initial taxonomic revisions based on our results as a start to revising the complex taxonomy of *Dryocosmus*. We consider that these revisions can safely be made without the "root and branch" revision required to

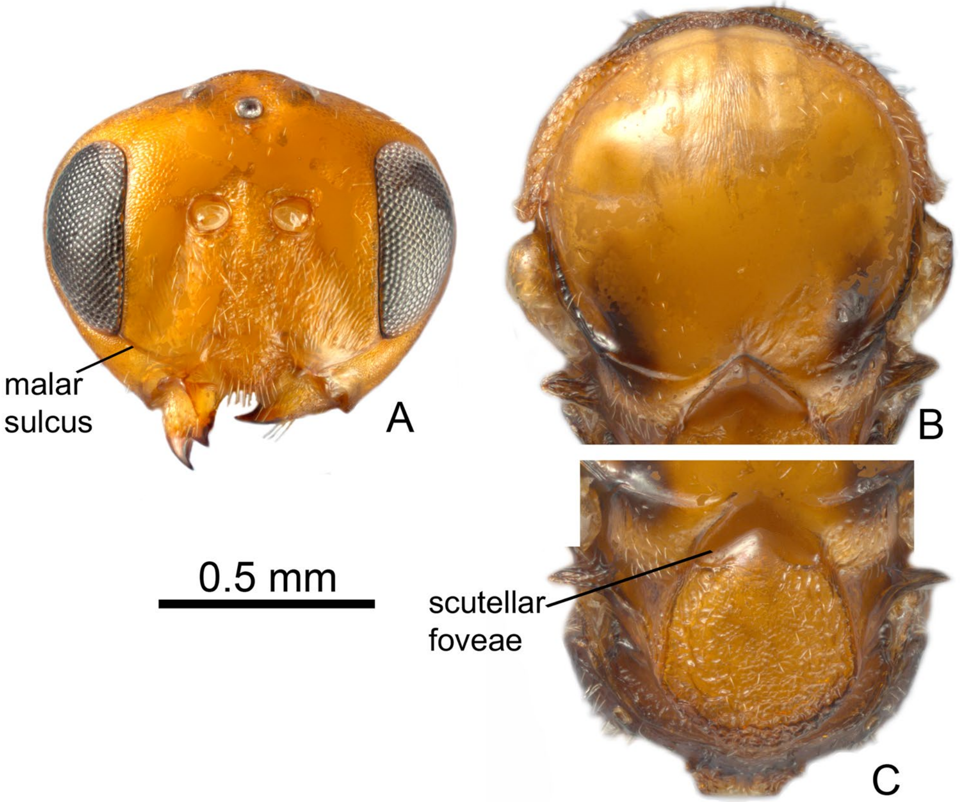


Fig. 5. Morphological characters of *Neuroterus asymmetricus* (Kinsey), **comb. nov**. A) head, frontal view. B) mesoscutum, dorsal view. C) scutellar foveae and mesoscutellum, dorsal view.

resolve the generic status of *Callirhytis*, *Dryocosmus*, and other problematic genera (see Discussion).

Transfer of *D. asymmetricus* to *Neuroterus*

Both the StarBEAST and ML phylogenetic analyses clustered *D. asymmetricus* with 2 Nearctic *Neuroterus* species (node 10; Fig. 4 and Supplementary Fig. S3). Morphological reassessment of *D. asymmetricus* indicates that it shares the following diagnostic characters in common with the genus *Neuroterus*: malar sulcus is present (Fig. 5A); notaulus is indistinct and only superficially impressed on anterior 1/4 of mesoscutum (Fig. 5B); transscutal articulation is absent (Fig. 5B); mesoscutellar foveae are fused together and are in the form of a transverse, impressed anterior area, with a smooth and glabrous bottom (Fig. 5C). These character states are inconsistent with those used to define *Dryocosmus* (see Introduction). Hence, we transfer *D. asymmetricus* to *Neuroterus* as *Neuroterus asymmetricus* (Kinsey 1922), **comb. nov.**

Reinstatement of the Combination *D. kunugiphagus*

Our phylogenetic analyses placed *P. kunugiphagus* in the same well-supported grouping as the type species of *Dryocosmus*, *D. cerriphilus* (node 2; Fig. 4 and Supplementary Fig. S3), while other *Plagiotrochus* species formed a well-supported cluster in a phylogenetically distant part of the C clade. *Plagiotrochus kunugiphagus* was originally described in the genus *Dryocosmus* (Ide and Abe 2015) with the acknowledgement that it displayed some morphological characters consistent with placement in either genus. Pujade-Villar et al. (2020) then transferred it to *Plagiotrochus*, citing multiple characters in support of this placement, although some characters states they provided are noted as being "sometimes" or "rarely" present in either genus, consistent with our observation above that some ambiguous traits are used in definitions of Cynipini genera. Given this morphological uncertainty but the strong molecular phylogenetic signal, we transfer this species back into the genus it was first described in, as *Dryocosmus kunugiphagus* Ide and Abe **comb. rev.**

Description of a New Genus for *Chrysolepis*-Associated *Dryocosmus* Species

Four species of *Dryocosmus* induce galls on the host plant genus *Chrysolepis* on the Pacific slope of North America. These form a clearly distinct clade in both StarBEAST and ML analyses (node 8; Fig. 4 and Supplementary Fig. S3), consistent with other studies that show this set of species to be allied to *Heteroecus* Kinsey and *Grahamstoneia* Melika and Nicholls, and not with other *Dryocosmus* taxa (Nicholls et al. 2018, Melika and Nicholls 2021).

Here we establish the new genus, *Chrysolepicynips* Stone, Nicholls, Melika and Tang, **gen. nov.** to circumscribe the four *Chrysolepis*-associated *Dryocosmus* species, with four new combinations: *Chrysolepicynips castanopsidis* (Beutenmuller 1917), **comb. nov.**, *C. demartinii* (Melika, Nicholls and Stone 2018), **comb. nov.**, *C. juliae* (Melika, Nicholls and Stone 2018), **comb. nov.**, *C. rileypokei* (Morita and Buffington 2009), **comb. nov.**

Chrysolepicynips Stone, Nicholls, Melika and Tang, gen. nov.

LSID: urn: lsid: zoobank.org: act : 49D31DFC-9CE4-43E1-9BCD-ABEC6FE1D1BE

Type species. *Andricus castanopsidis* Beutenmuller, 1917.

Etymology. The new genus name combines a host plant association with the genus *Chrysolepis* with the suffix *-cynips*, widely used to indicate membership of the oak gallwasp tribe Cynipini.

Gender. Masculine.

Diagnosis. Both sexual and asexual generations of *Chrysolepicynips* **gen. nov.** have been described. Body sculpturing patterns of *Chrysolepicynips* **gen. nov.** in both generations mostly resemble *Dryocosmus*; however, *Chrysolepicynips* **gen. nov.** is distinguished from *Dryocosmus* by the following characters: (i) There are numerous white setae on the lower face, postgena and vertex; numerous white setae (much denser in *C. castanopsidis*, **comb. nov.**) also present on the following regions of the mesosoma: lateral pronotum, mesopleural triangle, the ventral area of mesopleuron, dorsal and lateral axillar areas, the area defined by metasomal sulcus and mesopleuron, metanotal trough and lateral propodeal area; second metasomal tergum has dense white setae basal-laterally, disrupted dorsally. (ii) Mesoscutellar fovea is divided by an elevated narrow central carina. (iii) The lateral propodeal carinae are sub-parallel.

Re-description. Asexual female. Head alutaceous to coriaceous, with white setae, denser on lower face, vertex, and postgena; broader than long in dorsal view, broader than high in anterior view. Gena slightly broadened behind the eye in dorsal view, as broad as diameter of eye in lateral view. Malar space with or without striae radiating from clypeus; if striae present, then reaching bottom margin of eye; malar sulcus absent. Eye taller than length of malar space. Inner margins of eyes parallel. Transfacial distance longer than height of eye and longer than height of lower face (distance between antennal rim and ventral margin of clypeus). Lower face delicately coriaceous, with white setae, median area not elevated. Clypeus trapezoid, broader than high, alutaceous to coriaceous, with deep anterior tentorial pits, distinct epistomal sulcus and clypeo-pleurostomal line; ventrally straight, not emarginate, not incised medially, with dense long setae reaching far beyond ventral margin of clypeus. Frons alutaceous to delicately coriaceous, with rare short setae; vertex, interocellar area, and occiput alutaceous to delicately coriaceous with rare short white setae. Postgena coriaceous, glabrous, with dense setae. Postocciput around occipital foramen impressed, smooth, glabrous, without striae along occiput; posterior tentorial pits large, deep, and elongate. Antenna with 12 flagellomeres.

Pronotum smooth, glabrous, with white setae and without striae laterally. The anterior rim of the pronotum narrow, emarginate; propleuron alutaceous, with a few setae, and strongly concave in the mediocentral part. Mesoscutum smooth, glabrous between notauli, alutaceous laterad to notaulus; longer than broad (width measured across base of tegulae); notauli complete, deeply impressed along full length; median mesoscutal line distinct, broad; anterior parallel lines invisible or distinct in anterior ¼ of mesoscutum; parapsidal lines visible; parascutal carina broad, anteriorly reaching notaulus. Transscutal articulation deep, distinct, and straight. Mesoscutellum uniformly rugose, overhanging metanotum; scutellar foveae transversely ovate, with glabrous, smooth bottom, divided by narrow central elevated area. Mesopleuron smooth, glabrous, with white, dense setae along ventral and anterior margins; speculum smooth, glabrous; mesopleural triangle coriaceous, glabrous, with numerous to dense white setae. Dorsal and lateral axillar areas glabrous, alutaceous, with dense white setae; metanotal trough glabrous, smooth, with numerous to dense white setae. Lateral propodeal carinae distinct, sub-parallel, central propodeal area smooth, glabrous, without rugae; lateral propodeal area alutaceous, with dense white setae obscuring the surface sculpture. Tarsal claws simple, without basal lobe.

Forewing longer than body, hyaline, with distinct brown veins, margin with long dense setae; radial cell open along anterior margin; areolet large, triangular, closed, and distinct; Rs+M nearly reaching basalis halfway along its height.

Metasoma slightly longer than head+mesosoma, as long as high in lateral view, smooth, and glabrous; 2nd metasomal tergum with dense white setae anterolaterally, setae absent dorsally; all subsequent terga without setae; prominent part of ventral spine of hypopygium very short, 2.0× as long as broad in ventral view, with long white setae extending beyond apex of spine but never forming a tuft.

Detailed morphological descriptions for the asexual generations of *C. castanopsidis*, **comb. nov.**, *C. demartinii*, **comb. nov.** and *C. rileypokei*, **comb. nov.** are provided in Nicholls et al. (2018). The gall of the asexual generation of *C. juliae*, **comb. nov.** has been confirmed using DNA sequences, but the adults have not been reared yet (Nicholls et al. 2018).

Sexual generation. Males resemble females of the sexual generation. Both sexes of the sexual generation also resemble asexual females, although setae on the head and mesosoma (as outlined in the diagnosis) are less dense in the sexual generation. Male antenna has 13 flagellomeres, while the female antenna has 12 flagellomeres. The prominent part of the ventral spine of the hypopygium at most 2.5× longer than broad in ventral view.

Detailed morphological descriptions of sexual generation adults of *C. juliae*, **comb. nov.** and *C. rileypokei*, **comb. nov.** are provided in Buffington and Morita (2009) and Nicholls et al. (2018).

Distribution and biology. All *Chrysolepicynips* species are known only from California, and both generations induce galls on *Chrysolepis* (Fig. 3). Asexual generation galls are induced on buds (*C. demartinii* and *C. rileypokei*) or catkins (*C. castanopsidis* and *C. juliae*); known sexual generation galls are induced in fruit cupules (*C. rileypokei*) and buds, leaves, and young shoots (*C. juliae*) (Nicholls et al. 2018).

Remarks. *Chrysolepicynips* **gen. nov.** is phylogenetically closely allied to the 2 Nearctic genera *Grahamstoneia* and *Heteroecus* (Melika and Nicholls, 2021); however, the 3 genera are distinguishable in terms of body sculpturing pattern, setation on the lateral propodeal area, and the prominent part of the ventral spine. Reticulate sculpture on the head and mesosoma is only present in *Grahamstoneia*, not in *Chrysolepicynips* **gen. nov.** or *Heteroecus*. Setation on the lateral propodeal area of *Heteroecus* is less dense, and the surface sculpture is clearly visible; setation on the lateral propodeal area of *Chrysolepicynips* **gen. nov.** and *Grahamstoneia* is much denser and obscures the surface sculpture. The prominent part of the ventral spine in *Heteroecus* is 3.0–4.0× as long as broad, longer than *Chrysolepicynips* **gen. nov.** (at most 2.5× as long as broad) and *Grahamstoneia* (1.0× as long as broad).

Generation Matching in *Dryocosmus*

In our phylogenetic analyses, sexual generation *D. quercusnotha* (Fig. 6A and B) and asexual generation *C. furva* (Fig. 6C) grouped together with near-identical sequences (Fig. 4). Both of these species were originally described from the section *Lobatae* oak *Q. palustris* (Osten Sacken 1870, Weld 1952a), and our sampling was also from the same host plant species. *Dryocosmus quercusnotha* was originally described in the genus *Cynips* and was later transferred to *Dryocosmus* by Weld (1959), while *C. furva* has not been subject to nomenclatural change. The most probable explanation for their phylogenetic proximity is that, although currently in different genera, these 2 taxa represent the 2 generations of a single biological species. In the additional individuals we sequenced for cytb and ITS2 (see Methods), the observed levels of divergence both in cytb (0.00% to 0.69%) and ITS2 (0.00% to 0.02%) fall within the expected range for within-species variation in Cynipini (Melika et al. 2021a, Nicholls et al. 2022), confirming closure of the lifecycle. We hereby synonymize *Callirhytis furva* Weld, 1952, **syn. nov.** as the junior synonym of *D. quercusnotha* (Osten Sacken 1870).

Likewise, *D. quercuslaurifoliae* (Fig. 6D and E) and *D. quercuspalustris* (Fig. 6G and H) (both known only from a sexual generation) and *Z. guttatum* (Fig. 6F and I) (known only from an asexual generation) clustered together (Fig. 4), and again probably represent the 2 generations of a single species (in contrast to Ward et al.'s 2022 conclusion—see Discussion). *Dryocosmus quercuslaurifoliae* was first described from *Q. laurifolia* Michx. in Florida by Ashmead (1881) in the genus *Spathegaster* (now a synonym of genus *Neuroterus*) and later was also recorded galling *Q. phellos* (Weld, 1959). *Dryocosmus quercuspalustris* was first described from *Q. palustris* by Osten Sacken (1861) in the genus *Cynips*. Both species were transferred to *Dryocosmus* by Weld (1959). The distinction between *D. quercuslaurifoliae* and *D. quercuspalustris* in Weld (1959) was based on their associations with different oak hosts—*D. quercuslaurifoliae* galls *Q. laurifolia* and *Q. phellos*, and *D. quercuspalustris* galls *Q. palustris* and other red oaks. One of us (CTT) examined the gall morphologies and adult morphology of these sexual generation galls collected from both *Q. phellos* and *Q. palustris*. Gall morphologies of both species are identical, with a hollow inner space and a free-rolling larval cell; morphological characters of adults are also indistinguishable. In the additionally sequenced individuals for cytb and ITS2 (see Methods), the observed levels of variation for cytb (0.00% to 1.84%) and ITS2 (0.00% to 0.08%) again fall within expected within-species limits (Melika et al. 2021a, Nicholls et al. 2022). We thus synonymize the 3 species as *Dryocosmus quercuspalustris* (Osten Sacken 1861), with *Dryocosmus quercuslaurifoliae* (Ashmead 1881), **syn. nov.** and *Zopheroteras guttatum* Weld, 1952, **syn. nov.** as junior synonyms.

Transfer of *C. congregata* to *Melikaiella*

The phylogenetic analyses grouped *Callirhytis congregata* (Ashmead) with another species galling section *Lobatae* oaks, *Melikaiella tumifica* (Osten Sacken) (node 11; Fig. 4 and Supplementary Fig. S3). Morphological assessment of the syntypes (see http://n2t.net/ark:/65665/3d4d86223-0789-4612-b281-a1cdd9a35b4a, http://n2t.net/ark:/65665/3cff1e120-d6e1-436d-a024-4afa12908d79) also indicates that *C. congregata* is incorrectly placed in *Callirhytis* but instead has characters consistent with the delimitation of the genus *Melikaiella*: circumscutellar carina is present; metasomal tergites with areolate surface sculpturing is present in both male and female; rugose rather than transversely carinate sculpturing present on

Fig. 6. Galls of alternate sexual and asexual generations of *Dryocosmus* associated with section *Lobatae* in *Quercus* that are matched in this study. A–C) *D. quercusnotha* galls on *Q. palustris*: A, *D. quercusnotha* sexual gall; B, sexual gall opened to show the free-rolling and pointed larval cell inside; C, *D. quercusnotha* (= *C. furva* **syn. nov**.) asexual gall. D–I) *D. quercuspalustris* galls: D, sexual *D. quercuspalustris* gall on *Q. phellos* (= *D. quercuslaurifoliae* **syn. nov**.); E, sexual gall on *Q. phellos* opened to show the free-rolling larval cell and newly emerged adult; F, asexual *D. quercuspalustris* (= *Z. guttatum* **syn. nov**.) gall on *Q. phellos*; G, *D. quercuspalustris* sexual gall on *Q. palustris*; H, sexual gall of *D. quercuspalustris* on *Q. palustris* opened to show the round free-rolling larval cell inside; I, asexual *D. quercuspalustris* (= *Z. guttatum* **syn. nov**.) gall on *Q. palustris*. All scale bars are equal to 5 mm.

mesoscutum; no carinae are radiating from clypeus across the lower face (Pujade-Villar et al. 2014). Hence, we transfer *C. congregata* to *Melikaiella* as *Melikaiella congregata* (Ashmead 1896), **comb. nov.**

Transfer of *C. clavula* to *Andricus*

Our phylogenetic analyses placed *Callirhytis clavula* (Osten Sacken) into a well-supported clade containing the species *Andricus cinnamomeus* Ashmead and *A. hakonensis* (Ashmead) (node 12; Fig. 4 and Supplementary Fig. S3); this clade is sister to *A. kollari* (Hartig), a species from the monophyletic host-alternating *Andricus* lineage (Stone et al. 2009). Although our analyses did not include the type species of *Andricus*, *A. quercusradicis* (Fabricius), previous phylogenetic analyses involving that species demonstrated that *A. quercusradicis* and *A. cinnamomeus* are closely related and in the sister lineage to host-alternating *Andricus* (Cuesta-Porta et al. 2022, 2023), implying that *C. clavula* will also be a close relative of *A. quercusradicis*. This species has at various times been classified within either *Callirhytis* or *Andricus* (most recently in *Callirhytis*; Weld 1952b, Burks 1979), but placement of many Nearctic species into either *Andricus* or *Callirhytis* has historically been confusing and based on a poor morphological character (see Melika and Abrahamson 2002). However, in the case of *C. clavula*, the molecular data provide more compelling evidence of genus-level assignment pending a much more extensive reassessment of the morphological limits of Nearctic *Callirhytis* and *Andricus* lineages. Hence, we transfer it back to *Andricus* as *Andricus clavula* (Osten Sacken 1865), **comb. rev.**

Conclusions

Dryocosmus is a massively polyphyletic genus that contains four major groups of species associated with different host plant lineages: *Chrysolepis*, *Castanopsis*+*Castanea*, *Quercus* section *Cerris*, and *Quercus* section *Lobatae*. In the latter group, *Dryocosmus* species are intermingled with *Callirhytis* and *Zopheroteras* species, and this group as a whole is closely allied to *Kokkocynips*. The section *Cerris*-associated group additionally contains some well-defined accepted genera that also gall this oak lineage. In addition to these 4 major lineages, *Dryocosmus* also contains multiple lineages containing only 1 or a few species, sometimes with clear affinities to other described genera. It is clear that some Nearctic species have been placed in *Dryocosmus* arbitrarily, despite possessing incompatible states for diagnostic characters.

We propose that 3 of the 4 host plant-associated lineages plus a subset of species from the *Cerris*-associated clade represent biologically meaningful natural groups and recommend that future taxonomic work should erect new genera for these lineages. The name *Dryocosmus* should be retained solely for the type species and closely allied taxa, potentially also subsuming the genus *Aphelonyx*. Such revisions will also require reassessment of other genera with which *Dryocosmus* species are currently intermixed phylogenetically—particularly *Aphelonyx*, *Callirhytis* and *Zopheroteras*. This taxonomic work will require extensive morphological and molecular assessment of species additional to those sampled in the current study, but herein we start this process with some clearly distinguishable *Dryocosmus* taxa. Additionally, to avoid expanding existing taxonomic confusion, the description of any new putative *Dryocosmus* and *Callirhytis* species should include sequence-based allocation to a specific lineage in the Cynipini (eg, Fang et al. 2020, Melika et al. 2021b, Nieves-Aldrey et al. 2021). This in turn should facilitate the identification of morphological criteria for the stable definition of Cynipini genera.

Specimen Collection Statement

Nagoya Protocol: The authors attest that all legal and regulatory requirements, including export and import collection permits, have been followed for the collection of specimens from source populations at any international, national, regional, or other geographic level for all relevant field specimens collected as part of this study.

Nomenclature

This paper and the nomenclatural act(s) it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:EA4F00A6-1440-42D2-A640-E526DC8DEB62.

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Author Contributions

Chang-Ti Tang (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Funding acquisition [equal], Investigation [equal], Project administration [lead], Validation [equal], Visualization [lead], Writing—original draft [lead], Writing—review & editing [equal]), James Nicholls (Conceptualization [equal], Data curation [equal], Funding acquisition [equal], Investigation [equal], Project administration [equal], Validation [equal], Writing—review & editing [equal]), George Melika (Conceptualization [equal], Investigation [equal], Resources [equal], Writing—review & editing [equal]), Matthew Buffington (Funding acquisition [lead], Resources [equal], Supervision [equal], Writing—review & editing [equal]), Michael Gates (Funding acquisition [lead], Resources [equal], Supervision [equal], Writing—review & editing [equal]), John Lill (Funding acquisition [equal], Resources [equal], Supervision [equal], Writing—review & editing [equal]), Carol Mapes (Investigation [equal], Resources [equal], Writing—review & editing [equal]), Man-Miao Yang (Funding acquisition [lead], Resources [equal], Supervision [equal], Writing—review & editing [equal]), Yoshihisa Abe (Investigation [equal], Resources [equal], Writing—review & editing [equal]), and Graham Stone (Conceptualization [equal], Funding acquisition [lead], Investigation [equal], Resources [equal], Supervision [equal], Writing—review & editing [equal])

Supplementary Material

Supplementary material is available at *Insect Systematics and Diversity* online.

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Conflicts of Interest

None declared.

Data Availability

New sequences generated in this study will be made publicly accessible through Genbank. Accession numbers of new sequences for phylogenetic analyses are PQ963550–PQ963573 for cytb, PQ877196–PQ877257 for D2, PQ963653–PQ963719 for opsin and PQ963574–PQ963652 for wingless. Accession numbers of new sequences for generation matching are PQ963514–PQ963549 for cytb and PQ850950–PQ850973 for ITS2. Data matrices and phylogenetic trees generated and used in the analyses are deposited in the Edinburgh DataShare of University of Edinburgh (https://doi.org/10.7488/ds/7902).

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