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**A fully web-illustrated morphological phylogenetic study of
relationships among oak gall wasps and their closest relatives
(Hymenoptera: Cynipidae)**

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A fully web-illustrated morphological phylogenetic study of relationships among oak gall wasps and their closest relatives (Hymenoptera: Cynipidae)

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Abstract

Large morphological phylogenetics analyses are often poorly documented because of the constraints of traditional print journals, making it difficult to critically evaluate the data and build on it in future studies. We use modern information technology to overcome this problem in a comprehensive analysis of higher relationships among oak gall wasps and their closest relatives. Our morphological characters are documented by more than 2,000 images deposited in the open web image database Morphbank (<http://www.morphbank.net>), allowing one-click access from character and character state descriptions to the raw data.

The oak gall wasps (Cynipidae: Cynipini) form one of the largest specialized radiations of galling insects with almost 1,000 described species attacking oaks or oak relatives. According to previous morphological studies, the Cynipini form a monophyletic clade, the Woody Rosid Gallers (WRG), together with three small cynipid tribes (Diplolepidini, Eschatocerini, and Pediastidini). The WRG all attack woody representatives of the rosid clade of eudicots. Little was previously known about higher WRG relationships. We studied 54 exemplar taxa of WRG, including representatives from 34 of the 41 valid genera of oak gall wasps, and two outgroups. The study resulted in 308 characters, 283 from morphology and 25 from biology and distribution; most of these are original to the present paper.

Parsimony analyses supported the monophyly of three major WRG lineages: Diplolepidini + Eschatocerini, Pediastidini + *Paraulax*, and Cynipini. The poorly known South American genus *Paraulax*, developing in galls on *Nothofagus*, is moved from Cynipini to Pediastidini to reflect these results. The single Japanese species described in *Paraulax* by Shinji (types lost) is transferred to *Ceroptres* as *C. quereicola* (Shinji 1938) **comb. nov.** Two major lineages of oak gallers were recognized in most analyses: (1) the *Neuroterus*-group (*Neuroterus*, *Pseudoneuroterus*, the previously recognized genus *Trichagalma*, *Plagiotrochus*, possibly also Palearctic *Dryocosmus* and *Aphelonyx*+*Disholcaspis*); and (2)

the *Cynips*-group (*Cynips*, *Belonocnema*, *Atrusca*, *Acraspis*, *Philonix*, *Biorhiza* and *Trigonaspis*). The large and problematic genus *Andricus* was paraphyletic in some analyses and monophyletic in others, with *Disholcaspis spectabilis* being the sister to other Cynipini in the former case and European *Callirhytis* in the latter.

Our results suggest that WRG are conservative in their host plant preferences but there is no evidence for parallel insect-plant cladogenesis. Distributional patterns suggest a possible origin for the oak gall wasps in the Nearctic but the picture is otherwise complicated. Both heterogeneity, the cyclical alternation of sexual and parthenogenetic generations, and heteroecy, the use of different sections of *Quercus* as host for the two generations, appear to have evolved twice within the WRG.

Key words: Morphbank, Cynipini, Diplolepidini, Pediaspidini, Eschatocerini, taxonomy, phylogeny, host plant, distribution

Introduction

Despite rapid progress in the development of molecular techniques, morphological phylogenetics continues to play an important role in evolutionary studies. Surprisingly often, morphological characters can contribute significant phylogenetic signal even when combined with much larger sets of molecular characters (for an example involving gall wasps, see Nylander *et al.* 2004). Even when this is not the case, there is a growing interest in mapping comparative morphological data onto phylogenies to better understand the morphological adaptations characterizing different clades, and to provide morphological characters for identification purposes and for the placement of taxa that are difficult to sequence. Dating phylogenies using fossils is also becoming increasingly important, and it ultimately depends on an accurate understanding of how morphology can be used to place fossils.

Unfortunately, large morphological phylogenetics analyses are typically poorly documented because of the constraints of traditional print journals. This makes it difficult to critically evaluate the data and build on it in future studies, effectively slowing progress in this field. Modern information technology can be used to overcome this problem, as we show here in a comprehensive, largely morphology-based analysis of gall wasp relationships (Hymenoptera: Cynipidae). Our morphological characters are documented by more than 2,000 images deposited in the open web image database Morphbank (<http://www.morphbank.net>), which provides long-term archiving of, and stable URL links to, high-resolution biological images and collections of such images. Each character in our dataset is hyperlinked to the relevant set of images, allowing one-click access to information that is very close to the raw data on which our observations are based.

The gall wasps (Hymenoptera: Cynipidae) have long since drawn attention for their spectacular galls, especially those on oaks and roses, which even have common English names like the marble gall of *Andricus kollari* (Hartig) and the bedeguar gall of *Diplolepis rosae* (Linnaeus). These two species both belong to the woody rosid gallers (WRG), a lineage of gall wasps first established based on morphological evidence (Liljeblad & Ronquist 1998; Ronquist 1999). The WRG, the higher phylogeny of which forms the main focus of this paper, all make galls on woody plants of the eudicot subclass Rosidae. The WRG include the cynipid tribes Diplolepidini, Eschatocerini, Pediaspidini and Cynipini but exclude a few other cynipid species with a similar habit, namely the species of *Diastrophus* galling *Rubus* bushes, which belong to the otherwise herb galling tribe Aylacini. The WRG also exclude the phytophagous cynipid inquilines (gall guests) belonging to the tribe Synergini, most members of which inhabit galls induced by WRG.

As currently construed, the Cynipidae comprise only one extant subfamily divided into the six tribes mentioned above. Of the two tribes outside the WRG, the Aylacini and Synergini have around 170 species each. This leaves roughly 1,000 described species in the WRG tribes. In Diplolepidini, there are 55 species in two genera, *Diplolepis* and *Liebelia*, all inducing galls on roses. The three species of *Eschatocerus*, the single genus in the tribe Eschatocerini, are found on *Acacia* and *Prosopis* (Fabaceae). There are only two Pediaspidini species, of which the sycamore (maple) gall wasp, *Pediaspis aceris* (Gmelin), has its host in Sapindaceae