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CURRENT STATE OF KNOWLEDGE OF HETEROGONY IN CYNIPIDAE (HYMENOPTERA, CYNIPOIDEA)

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ABSTRACT

Current state of knowledge of heterogony in Cynipidae (Hymenoptera, Cynipoidea). Heterogony or alternation of generations characterises two tribes in Cynipidae: Pediaspidini (with 2 species) and Cynipini (with over 900 described species), but only for above 85 cynipid species life cycles are known.

In this paper we give data about Cynipini biology, a complete table of Cynipidae known or suspected life cycles and a historic review of studies on heterogony in this group. Proposed life cycle models and possible mechanisms of heterogony origination are discussed. Bibliography on this problem is given.

Key words: Hymenoptera, Cynipidae, Pediaspidini, Cynipini, heterogony, biological life cycles, review.

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RESUM

L'heterogònia o alternança generacional és característica de dos tribus de Cynipidae: Pediaspidini (amb 2 espècies conegudes) i Cynipini (amb més de 900 espècies descrites). Només uns 85 cicles són coneguts, per la qual cosa la majoria d'ells estan per descriure.

En aquest treball es donen dades referides a la biologia dels Cynipini, es fa un repàs històric del coneixement de la heterogònia en aquest grup d'himenòpters, es dónen dades dels diferents models que els caracteritzen, es dicuteix l'origen del caràcter heterogònic i s'esmenten aquells cicles coneguts a la bibliografia. També es donen dades de les referències bibliogràfiques referents a aquesta problemàtica.

INTRODUCTION

Cynipidae includes wasps which are characterised by their ability to induce galls on different plant hosts. They are currently divided into 6 tribes (Ronquist, 1999):

"Aylacini" galling different herbaceous plants, from Asteraceae, Papaveraceae, Lamiaceae, Valerianaceae and Apiaceae families (Nieves Aldrey 1994); Eschatocerini inducing galls on *Acacia* and *Prosopis*; Diplolepidini on *Rosa*; Pediaspidini on *Acer*, and Cynipini attack Fagaceae, mainly *Quercus*. Species included into the 6th tribe, Synergini, have lost their ability to induce galls and they live as phytophagous inquilines in Cynipini galls. Probably one of the most fascinating aspects in the group is their unique biology, that have attracted many scientists. Life cycles are diverse, reaching maximum complexity in some members of Cynipini tribe, the most speciouse tribe with over 900 species from 42 genera (Table 1). A complete review of different life cycles can be found in Folliot (1964) and Askew (1984) so we find unnecessary to detail it here. The "heterogony", or the alternation of asexual and sexual generations, restricted to Cynipini and Pediaspidini, is the main cycle model. Galls of the asexual generation are normally the most durable ones and normally are appearing during late summer-autumn, while galls of the sexual generation are ephemeral and can be found in spring and/or early summer. However, this aspect can be also strongly vary, and many exceptions can be find, for example, in *Andricus quadrilineatus* Hartig, 1840, a Western-Palaearctic species, both galls appear in spring (Folliot 1964), as well as the gall of *Dryocosmus kuriphilus* Yasumatsu, 1951, a species which is known from the asexual generation only (Abe, 1994).

NOMENCLATURE OF HETEROGONIC SPECIES

Morphological differences between asexual and sexual forms of the same species might be so strong that in the past, many times they were described as separate species or even in different genera (Melika & Abrahamson, 2000*a*). In fact many of the species known on the basis of one generation only might represent an unknown generation of another described species. In other cases the alternant generation is not known, and is normally the bisexual one, since their galls are small size, ephemeral and unconspicuous appearance.

To nominate a species, first specific names were conserved, even when included in different genera, for example, Adler (1881) found that the bisexual form of *Neuroterus lenticularis* (Olivier, 1791) was *Spathegaster baccarum* (Linnaeus, 1758) and he kept both names in his study. Later Mayr (1882) included both alternate forms in the same genus, including a morphological revision of specimens, but he continued to use specific names for both form, talking about *Neuroterus quercusbaccarum* (L., 1758) and *N. lenticularis* as independent forms. Posterior authors proposed only one name for each species, which would be the first described form (priority principle), and thus the species in the previous example was named *Neuroterus quercusbaccarum,* the oldest name, and to indicate different forms of the same species we would write *Neuroterus quercusbaccarum* s. f. and *Neuroterus quercusbaccarum* a. f., respectively. Kinsey (1920) proposed a trinominal system respecting the "priority principle (art. 23)", putting form name after specific name, thus according in the same example, we would be speaking about *Neuroterus quercusbaccarum* (Linnaeus) for the bisexual generation and *Neuroterus quercusbaccaru*m form *lenticularus* Olivier for the unisexual generation, respectively. Later Eady & Quinlan (1963) and Folliot (1964) used a similar system but the name of the alternate

Table 1. Genera of Cynipini from WELD (1952), with some considerations about them. Data about number of species from several authors.

Genus name	Geographic distribution	Number of species	Taxonomic status	Host sections of *Quercus*: Erytrobalanus = E Leucobalatus =L Protobalanus= P Cerris = C	Others Fagaceae hosts
Acraspis	*Nearctic*	*probably* > 30	MAYR (1881). Must be revised. Currently include species which probably belong to other genera.	L	
Amphibolips	Nearctic	around 30	REINHARD (1865). Must be revised, especially species described from Mexico by KINSEY (1937a, 1937b).	E, L	
Andricus (=*Adleria*)	Holarctic and Oriental?	probably > 300	HARTIG (1840); ROHWER & FAGAN (1917). This genus needs a deep revision. BENSON in MARSDEN-JONES (1953) synonymyzed *Adleria* genus. *Dros*, *Erhytres*, *Parandricus*, *Liodora* genera probably related to *Andricus* or might be synonyms.	E, L, P, C	*Lithocarpus densiflora*
Antron	*Nearctic*	*around* 40	Originally was described as a subgenus of *Cynips* (KINSEY, 1929); later WELD (1952a) gave to it genus status. This genus needs a deep revision, might be synonym of *Cynips*.	L, P	
Aphelonyx	Palaearctic	4	MAYR (1881). This genus needs a revision to confirm the Japanese species.	C	
Atrusca	Nearctic	uncertain; probably > 40	Originally was described as a subgenus of *Cynips* (KINSEY, 1929); later WELD (1952a) gave to it genus status. This genus needs a deep revision.	L	
Bassettia	USA	9	ASHMEAD (1887). Needs a revision, also new species are under description (Melika & Abrahamson, *in prep*.)	E, L	
Belizinella	Russia, Far East	2	KOVALEV (1965). Closely related to the Palaearctic *Trigonaspis* and North American *Xystoteras* genera and might be synonym of one of them. All these apterous and short winged genera need a strong revision.	*E*	
Belonocnema	USA	2	MAYR (1881).	E	
Besbicus	USA	8	Originally was described as a subgenus of *Cynips* (KINSEY. 1929); later WELD (1952a) gave to it genus status. This genus needs a deep revision, might be synonym of *Cynips*.	E, L	
Biorhiza	Palaearctic	2	WESTWOOD (1840). WELD (1952a) transferred the Nearctic species to different genera. *Biorhiza australiensis* Kieffer and *B. cecconiana* (Kieffer) are dubiously included in this genus.	L	
Callirhytis	Holarctic	around 150	FOERSTER (1869). This genus needs a revision. Many North American species placed in this genus probably belong to the *Andricus* or other genera.	E, L, P, C	
Chilaspis	Occidental Palaearctic	3	MAYR (1881). Revision in Pujade-Villar, Ros-Farré & Melika (in prep.)	C	
Cynips	Palaearctic	around 25	LINNAEUS (1758). This genus needs a revision. North American *Antron* and *Besbicus* are very closely related, also species described from the Far East of Russia (KOVALEV 1965) and Transcaucasus (BELIZIN 1961; MAISURADZE 1961, 1962) must be revised.	L, C	
Disholcaspis	Nearctic	around 40	DALLA TORRE & KIEFFER (1910).	E, L, P	
Dros	Nearctic	11	KINSEY (1937a). This genus needs a revision because some species are probably confused with *Andricus* and *Liodora* genera.	L	
Dryocosmus	Holarctic	around 25	GIRAUD (1959). This genus needs a revision. Probably some species, especially from North America, belong to other genera.	C	*Castanopsis* ssp, *Castanea* spp
Erythres	Mexico	2	KINSEY (1937b). The validity of this genus is dubious. Related to *Andricus*.	E	
Eumayria (=*Trisoleniella*)	USA	5	ASHMEAD (1887); ROHWER & FAGAN (1917). Revision in MELIKA & ABRAHAMSON (1997b); junior synonymy in the same paper.	E	
Eumayriella	USA	2	Description in MELIKA & ABRAHAMSON (1997b)	E	
Euxystotheras	USA	1	LYON (1993). Closely related to Phylloteras genus; its validity is dubious.	*E*	
Heteroecus	USA	15	KINSEY (1922). The validity of this genus is dubious.	P	
Holocynips	USA	4	KIEFFER (1910). The validity of this genus is dubious.	E, L, P	
Liodora	USA	3	FOERSTER (1869). The validity of this genus is dubious. Related with *Andricus*.	L	
Loxaulus	Nearctic	14	MAYR (1881). Revision in MELIKA & ABRAHAMSON (2000b).	E, L, P	
Neoneuroterus	Russia, Far East and Japan	5	MONZEN (1954). The genus must be revised.	L, C	
Neuroterus	Holarctic	about 100	HARTIG (1840). This genus need a revision. KINSEY (1923, 1936) divided the genus into several subgenera that could be valid. *Latuspina* described by MONZEN (1954) from Japan can also be a different genus (WELD 1964) and must be revised.	L, P, C	
Odontocynips	USA	1	KIEFFER (1910). The genus with undescribed species was found in Costa Rica (P-V, J., unpubl. data).	L	
Paracraspis	USA	3	WELD (1952b). The validity of this genus is dubious. Closely related to *Acraspis*.	P	
Parandricus	China	1	KIEFFER (1906). The validity of this genus is dubious. Closely related to *Andricus*.	Unknown oak	
Paraulax	Chile and Japan	1	KIEFFER (1904). Several undescribed species and probably not correctly placed in Cynipini tribe (Ronquist, *pers. com.*).		*Nothophagus* sp
Philonix	USA	8	FITCH (1859/1958). Must be revised.	L	
Phylloteras (= *Xystoteras*)	Nearctic	6	ASHMEAD (1897a); ASHMEAD (1897b). LYON (1993) synonymyzed *Xystoteras*.	E, L	
Plagiotrochus (=*Fioriella*)	Palaearctic occidental and Hymalaya	14	MAYR (1881); KIEFFER (1903). MELIKA *et al.* (2001) synonymyzed *Fioriella* genus. BELLIDO *et al* (2000) mentioned *Plagiotrochus* genus in Himalayan area.	C	
Repentinia	Central Europe and Azerbajan	1	Genus described by Belizin & Maisuradze in MAISURADZE (1961). Supposedly the correct name of this genus must be *Pseudoneuroterus* (currently a subgenus of *Neuroterus*, proposed by KINSEY (1923); revised by Pujade-Villar *et al* (*in prep*.).	C	
Sphaeroteras	USA	8	ASHMEAD (1897a). The validity of this genus is dubious. Closely related to *Biorhiza*.	E, L	
Trichagalma	Japan and China	2	MAYR (1907). The asexual generation only is known. The genus closely related to *Repentinia* and *Neuroterus*.	C	
Trichoteras	USA	8	ASHMEAD (1897a). The validity of this genus is dubious; closely related to the *Andricus* genus.	E, L, P	
Trigonaspis	Palaearctic	Around 10	HARTIG (1840). The species described in the oriental Palaearctic need to be revised. NIEVES-ALDREY (1990) revised the European fauna. See also comments to *Belizinella*, *Ussuraspis*, *Xystoteras*, *Xanthoteras* genera.		
Ussuraspis	Russia, Far East	1	KOVALEV (1965). Closely related to the Palaearctic *Trigonaspis* and North American *Xystoteras* and *Xanthoteras* genera and might be synonym of one of them. All these apterous and short winged genera need a revision.	Q	
Xanthoteras	USA	12	ASHMEAD (1897b). The validity of this genus is dubious.	E, L	
Zopheroteras	USA	6	ASHMEAD (1897b). Needs a revision, also new species are under description (Melika & Abrahamson, *in prep*.)	E, L	

form come in parenthesis, thus the asexual form would be named for the same example as *Neuroterus quercusbaccaru*m f. a. (=*lenticularis* Olivier).

According to the International Code of Zoological Nomenclature (ICZN) (art. 23.1 and 23.3.2.2) only one specific name is valid for both generations of the same species and thus when closing the life cycle of a cynipid species the new sexual or asexual form should not be named because it will run into synonymy (art. 15.2). Moreover, definitive denomination of the species follows also “priority principle”. In the case both forms are known and have received different names and both have been described prior to 1960 (art. 15.2

and 45.6.3), and only in this case, the trinominal mode proposed by Eady & Quinlan (1963) is often used an so the alternate form is not indicated because the latin names indicate so [eg. *Neuroterus quecusbaccarum* (= *lenticularis*) was de name of the alternate generation of *Neuroterus quecusbaccarum*]. Always, the names proposed for alternate forms after this date are automatically regarded as synonyms of the nominal form.

HISTORY

Heterogony or alternation of generations in Cynipini was discovered, independently, in United States by Bassett (1873) and Riley (1873). However Osten Sacken (1861) suspected alternation of generations in *Callirhytis quercusfutilis* (Osten Sacken, 1861) and *Amphibolips confluens* (Harris, 1841). Later, Walsh (1864) supported the idea about alternate generations in *Amphibolips confluens*, but no direct experiments were carried out and so first "clear" demonstration of a life cycle in Cynipini is due to Bassett (1873) (after Wehrmaker, 1998). In Europe Bassett's results were passed unnoticed during some years and Adler (1877, 1881) reached the same conclusions and closed life cycles for some European species of Cynipini.

In some cases, studies on life cycles were taken by some specialists with scepticism, as in the case of Walsh's studies on *Amphibolibs confluens* in United States or Adler's conclusions on *Andricus kollari* (Hartig, 1843) in Europe. Life cycle of *A. kollari* was closed by Beijerinck (1902), but it was not accepted until it was confirmed experimentally by Marsden-Jones (1953).

In other cases, circumstancial evidences, made specialists to suspect alternate generations, although life cycles have never been supported experimentally. For example, *Plagiotrochus quercusilicis* s. f. (Fabricius, 1798) and *Plagiotrochus kiefferianus* a. f. Tavares, 1901 since Tavares (1926). In some cases these evidences are so old that were considered as a fact, like in *Chilaspis nitida* (Giraud, 1959) a. f. and *Chilaspis loewii* Wachtl, 1882 s. f. (Schlechtendal, 1888; Kieffer, 1897-1901). However, these statements without experimental studies are always dangerous, since sometimes are uncertain, and in some cases they have proved to be erroneous like in *Cynips quercus* (Fourcroy, 1785) a. f. and *Cynips flosculi* Giraud, 1968 s. f. (Pujade-Villar, 1991; Melika *et. al.,* 2000); in *Andricus corruptrix* (Schlechtendal, 1870) and *Andricus larshemi* (D. v. Leeuwen, 1956) (Folliot *et al*., *submited*). Moreover, recently an extraordinary specific difference have been brought to light: identical galls of asexual females correspond to different sexual forms located in different hosts, as in the case of *Andricus kollari* and *Andricus hispanica* (Hartig, 1856) (Pujade-Villar, 1992; Stone *et. al.,* 2001; Pujade-Villar *et al*, in prep.), and of *Andricus mukaigawae* (Mukaigawa, 1913) and *A. kashiwaphilus* Abe, 1998 (Abe, 1988, 1991 & 1998). So, in our opinion, without experimental evidences, is better do not establish strong relations between alternate generations, however, they can be used as an orientative basis for further research.

When the life cycle of a gall-inducing cynipid requires two different oak host species, the model is known as heteroecy, and can be find in a restricted number of Cynipini species belonging to *Callirhytis* Förster, 1869 and *Andricus* Hartig, 1840 genera.

Table 2. Alternation of generations in Cynipidae (Cynipoidea). Authors who closed the life cycles for certain species are indicated. Valid species names are given in *italics* if both, asexual and sexual generations have been nominated. (*) Asexual and sexual generations' "pairing" must be revised; (**) "pairing" of generations uncertain or suspected, do not closed experimentally; (***) doubtfull cycle, in the case of Kinsey, when he established the correspondence between two generations (forms) without experimental approvement.

KNOWN LIFE CYCLES IN PEDIASPIDINI AND CYNIPINI

Agamic form	Sexual form	Bibliographical references
PEDIASPIDINI		
Pediaspis		
sorbi (Tischbein)	*aceris* (Gmelin)	Mayr (1881), Adler (1881), Folliot (1964)
CYNIPINI		
Acraspis		
erinacei Beutenmueller	bicolens (Kinsey)	Triggerson (1914), Kinsey (1920)
gemula Bassett	known; not named	Kinsey (1929)
Amphibolips		
confluenta (Harris)	known; not named ?	Osten Sacken (1861)
globus Weld	known; not named	Weld (1952a)
Andricus[1]		
known; not named	*chrysolepidicola* (Ashmead)	Burdick (1967)
alniensis Folliot	rupellensis Folliot	Folliot (1964)
atrimentus (Kinsey)	known; not named	Dailey & Sprenger (1973a)
autumnalis Hartig	*quercusramuli* (Linnaeus)	Adler (1881)*
bocagei Kieffer	*pseudoinflator* Tavares	Tavares (1919)**, Pujade-Villar (1993)
callidoma (Hartig)	cirratus Adler	Adler (1881), Folliot (1964)
collaris Hartig	*curvator* Hartig	Adler (1881)
corruptrix (Schlechtendal)[2]	known; not named	Folliot *et al* (2001, *submited*)
crenatus Weld	*gigas* Kinsey	Dailey & Sprenger (1973b)
crystallinus Bassett	known; not named	Doutt (1960)
dentimitratus (Rejto)	known but not described	Pujade-Villar (1994), Pujade-Villar *et al* (2000)
fecundatrix (Hartig)	pilosus Adler	Adler (1881)
gallaeurnaeformis Fonsc.	sufflator Mayr	Mayr (1882)**, Folliot (1964)
gemmeus (Giraud)	known; not named	Pfützenreiter, 1962
giraudianus D. T. & Kieffer	*amenti* Giraud	Folliot (1964)
glandulae (Schenck)	xanthopsis Schlechtendal	Schlechtendal (1884)*, Niblett (1939)
globuli Hartig	*inflator* Hartig	Adler (1881)
hispanica (Hartig)[3]	known but not described	Pujade-Villar (1992)
hystrix Kieffer	known but not described	Folliot & Pujade-Villar (*unpublished*)
kashiwaphilus Abe	known; not named	Abe (1998)
kingi Bassett[9]	known; not named	Rosenthal & Koehler (1971)
kollari (Hartig)	circulans Mayr	Beijerinck (1902), Folliot (1964)
lignicolus (Hartig)	vanheurni D. v. L. & D.-M.	Drs. van Leeuwen & Dekhuijzen-Maasland (1958)
malpighi Adler[4]	nudus Adler[4]	Adler (1881), Pujade-Villar & Melika (2000)
mukaigawae (Mukaigawa)	known; not named	Abe (1986, 1988, 1991)
opertus (Weld)	fimbrialis Weld	Evans (1972)
paradoxus (Radoskovsky)	barbotini Folliot	Folliot (1964)
quadrilineatus Hartig	kiefferi Pigeot	Folliot (1964)
quercuscalicis (Burgsdorf)	cerri Beijerinck	Beijerinck (1897)
quercuscorticis (L.)	gemmatus Adler	Adler (1881), Folliot (1964)
quercusradicis (Fab.)	trilineatus Hartig	Adler (1881), Folliot (1964)
rhizomae (Hartig)[5]	*testaceipes* Htg. var *nodifex* Kief.	Adler (1881)
sieboldi Hartig[6]	poisoni Folliot[6]	Folliot (1964); Pujade-Villar (1986)
solitarius (Fonscolombe)	occultus Tschek	Docters van Leeuwen (1934)
symbioticus Kovalev	known; not named	Abe (1986)
targionii (Kieffer)	without sexual form	Weih (1965), Abe (1986)

Antron		
douglasii (Ashmead)	lobata McCracken & Egbert	McCracken & Egbert (1922)
quercusechinus (Osten Sacken)	ribes (Kinsey)	Kinsey (1922)
schulthessae Kinsey	atrata Kinsey	Kinsey (1929)
vicinum Kinsey	incepta Kinsey	Kinsey (1929)
Bassettia		
ligni Kinsey	known; not named	Rosenthal & Koehler (1971)
Belonocnema		
treatae Mayr	floridanus (Ashmead)	Lund, Ott & Lyon (1998)
Besbicus		
mirabilis	known; not named	Evans (1967)
Biorhiza		
aptera Fabricius	*pallida*(Olivier)	Adler (1881), Folliot (1964)
nawai (Ashmead)	known; not named	Yasumatsu & Matsuda (1955)
Callirhytis		
acorn gall on *Q. ilicifolia*	*illustrans* Kinsey	Kinsey (1922) ***
acorn gall on *Q. ilicifolia*	*falsus* Kinsey	Kinsey (1922) ***
acorn gall on *Q. marylandica*	*austrior* Kinsey	Kinsey (1922) ***
erythrocephala (Giraud)	hartigi Foerster	Nieves-Aldrey (1992)**
glandium (Giraud)	aestivalis Nieves-Aldrey	Barbotin *in* Nieves-Aldrey (1992)
glandulosa Weld	*rufescens* (Mayr)	Barbotin *in* Nieves-Aldrey (1992)
grumatus Weld	serricornis Kinsey	Lyon (1970)
milleri Weld	*flora* Weld	Dailey, Perry & Sprenger (1974)
eldoradensis (Beutenmueller)	known; not named	Dailey, Perry & Sprenger (1974)
quercusagrifoliae (Bassett)	known; not named	Lyon (1964)
quercuscornigera (Osten Sacken)	known; not named	Melika & Eliason (2001)
quercusoperatola (Bassett)	*quercusoperator* (Osten Sacken)	Bassett (1873)*
quercuspomiformis (Bassett)	known; not named	Lyon (1969)
quercussuttoni (Bassett)	known; not named	Lyon (1969)
radicicola (D. T. & Kieffer)	*quercusfutilis* (Osten Sacken)	Osten Sacken (1861)**, Bassett (1889)*
Chilaspis		
nitida Giraud	loewi Wachtl	Schlechtendal (1888)**, Kieffer (1897-1901)**
israeli Sternlicht [7]	known; not named	Sternlicht (1968)**
Cynips[8]		
agama Hartig	mailleti Folliot	Folliot (1964)
disticha Hartig	indistincta Niblett	Niblett (1948)
divisa Hartig	verrucosa Schlechtendal	Adler (1881)
longiventris Hartig[5]	similis Adler (=substituta Kinsey)	Adler (1881), Kinsey (1929)
quercusfolii Linnaeus	taschenbergi Schlechtendal	Adler (1881)
Disholcaspis		
cinerosa Bassett	known; not named	Frankie *et al* (1977*, 1984*)
eldoradensis (Beautenmueller)	known; not named	Evans (1972)
Dryocosmus		
attractans (Kinsey)	uvellae Weld	Dailey (1969)
bicornis McCracken & Egbert	*dubiosus* Fullaway	Doutt (1959)
cerriphilus Giraud	*nervosus* Giraud	Kieffer (1897-1901)**
kuriphilus Yasumatsu	without sexual generation	Abe (1994)
Heteroecus		
dasydactyli (Ashmead)	known; not named	Rosenthal & Koehler (1971)
pacificus (Ashmead)	known; not named	Lyon (1963)
Liodora		
pattersonae (Fullaway)	dumosae Kinsey[9]	Evans (1972)*

Loxaulus		
trizonalis Weld	known; not named	Weld (1926)
Neuroterus		
abundans Kinsey	*tectus* Bassett	Kinsey (1920)
anthracinus (Curtis)	furunculus Beijerinck	Beijerinck (1882)
contortus Weld	principalis Kinsey	Kinsey (1923) *
deprini Kinsey	*prini* Kinsey	Kinsey (1923) *
fumipennis Hartig	*tricolor* (Hartig)	Adler (1881)
hiemalis Kinsey	*pattersoni* Kinsey	Kinsey (1923) *
laevisculus Schenck	*albipes* (Schenck)	Adler (1881), Pujade-Villar (1985)
lenticularis Olivier	*quercusbaccarum* (Linnaeus)	Adler (1881)
numismalis (Fourcroy)	vesicatrix Schlechtendal	Adler (1881)
quercusbatatus Fitch	bisexualis Kinsey	Kinsey (1923)
(= *noxiosus* Bassett)	(= vernalis Kinsey)	Kinsey (1920), Melika & Abrahamson (1997a)
saliens (Kollar)	glandiformis Giraud	Barbotin (1972)
saltatorius (Edwards)	decipiens Kinsey	Rosenthal & Koehler (1971)*
politus Htg.	*petioliventris* Htg	Schlechtendal (1884)*, Folliot (1964)
(= schlechtendali Mayr)[10]	(= aprilinus Gir.) [10]	
twing galls without denomination	*washingtonensis* Beautenmueller	Evans (1972)
Philonix Fitch		
fulvicollis Fitch	pallipes (Bassett)	Kinsey (1929)**
Plagiotrochus[11]		
cabrerae Kieffer	*australis* (Mayr)	Barbotin (1975)
coriaceus (Mayr)	britaniae Barbotin	Pujade-Villar & Ros-Farré (1998)**
kiefferianus Tavares	*quercusilicis* (Fabricius)	Tavares (1926)**
razeti Barbotin	known; not named	Barbotin *In:* Melika *et al* (2001)
suberi Weld[12]	*amenti* Kieffer[12]	Nieves-Aldrey (1985)**
vilageliui Pujade-Villar	*panteli* Pujade-Villar	Pujade-Villar & Ros-Farré (1998)**
Trigonaspis		
renum Hartig	*megaptera* (Panzer)	Adler (1881)
synaspis (Hartig)	*megapteropsis* Wriese	Wriese *in* Kieffer (1897-1901)

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[1] *Andricus burgundus* Giraud has been considered by Beijerinck (*in* Dalla Torre & Kieffer, 1910) as the bisexual generation of *A. infectorius* but recent phylogenetic studies showed that these are two separate, unrelated species (Stone & Cook, 1998). In Melika *et al* (2000) mentioned than *A. ambiguus* has a sexual generation known but it is a mistake. We do not consider the relationship suspected by Kinsey (1920) between *Andricus compresus* (Gillette) a. f. and *Andricus quercuspalustris* (Osten Sacken) s. f. because the first one belongs to the genus *Zopheroteras* and the second one to the genus *Dryocosmus*.

[2] *Andricus larshemi* D van L. & D.- M. Is not the sexual form of *Andricus corruptrix* as stated by Docters van Leeuwen & Dekhuijzen-Maasland (1958).

[3] Unisexual form indistinguishable morphologically from *Andricus kollari* (Hartig) (Pujade-Villar & Bellido, 2000) but with a different sexual form (J.P-V unpublished; Pujade-Villar *et al*, *in prep*).

[4] See valid name of this species in Pujade-Villar & Melika (2000).

[5] See comments in Melika *et al.* (2000)

[6] Anteriorly sexual form was thought to be *Andricus testaceipes* Hartig; but see comments in Melika *et al.* (2000).

[7] See comments in "Review of the *Chilaspis* genus (Hymenoptera: Cynipoidea: Cynipidae)" in Pujade-Villar, Ros-Farré & Melika (in prep.)

[8] The agamic form named *Cynips quercus* (Fourcroy) has the sexual form named *Cynips flosculi* Giraud (according to Kieffer (1897-1901); Dalla Torre & Kieffer, 1910; Eady & Quinlan (1963)) without experimentation; Melika *et al* (2000) consider it is not true.

[9] Rosenthal & Koehler (1971) were incorrect when they considered *Andricus dumosae* as the bisexual generation of *A. kingi*; later Dailey and Menke (1980) found that the previous authors had misidentified '*dumosae*'. However Rosenthal and Koehler (1971) already found the bisexual generation of '*kingi*'.

[10] See review in Pujade-Villar & Ros-Farré (2001)

[11] The agamic forrn named *Plagiotrochus marianii* (Kieffer) has the sexual form named *Fioriella meunieri* Kieffer (according to Kieffer (1902; 1903a, 1903b)); Melika *et al* (2001) consider it is not true.

[12] See comments in Pujade-Villar (1998) and Pujade-Villar-Díaz (2001).

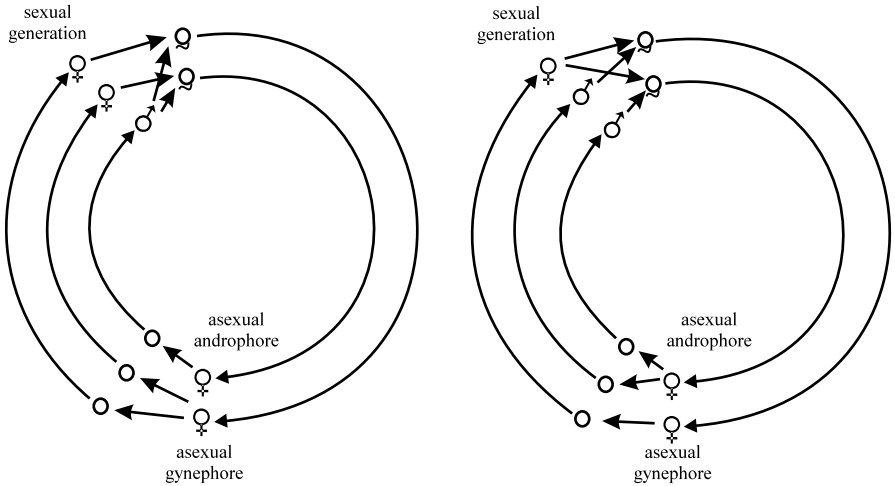

Figure 1. Sex determination models in heterogenous cynipid gall wasps (after FOLLIOT 1964 in ASKEW 1984). The classical theory (left) involves two types of sexual females. Folliot's theory (right) involves two types of sexual males.

Several authors, beside above-mentioned, have contributed to a better knowledge of the biology of this group (Table 2); although we would like to emphasize the great work done by Dr. R. Folliot, who closed life cycles for many European species of Cynipini. He described different life models and experimentally demonstrated several life cycles previously supposed but which were not closed in experimental conditions. The knowledge of the biology and life cycles of Cynipini in North America is far from that in Europe, however, we must mention works of Doutt, Kinsey, Lyon and Dailey, among others (Table 2).

HOSTS OF CYNIPINI

Many moments in the complex trophical relationships between gall wasps and their hosts are still unknown. One of the main factors effecting the distribution and abundance of Cynipini, without doubts, is their host plant (Stone *et al*, in prep.).

Diversity of oak species strongly influence the biodiversity of cynipids. For example, the reachest cynipid fauna throughout Europe can be find in Hungary – 95 species are listed (Melika, Csóka & Pujade-Villar, 2000) which trophically associated with 6 oak species. Diversity of oak cynipids is also high in the Mediterranean region, especially on the Iberian Peninsula where around 70 species associated with 11 oak species are present. By moving to north and east, oak's and Cynipini diversities becoming very poor and, for example, in Scandinavian countries where *Q. robur* only can be find in natural stands, only

39 cynipid species are registered (Coulianos & Holmasen, 1991). The same is happened by moving east- and north-eastward –in Leningrad Region of Russia where *Q. robur* only growth, 21 cynipid species were found (Vyrzhikovskaya, 1962), under the Ural Mountains (*Q. robur* only growth) only 14 species were registered (Vyrzhikovskaya, 1954). Heteroecous species are absent from these regions of Europe.

Although the niche specialisation seems to be strong and many cynipids are mainly "group host"-specific (Abrahamson *et. al.,* 1998a; 1998b), otherwords, the same species can attack different closely related oak species, which belongs to the same *Quercus* section, however, never go out of the boundaries delimited for the section. The Holarctic cynipids attacking white oaks never will develops on red oaks, and vice versa. More of that, within *Quercus* Sections there are very distinct species-groups, which with certain cynipid species trophically related (Abrahamson *et. al,.* 1998a; 1998b). Majority of Cynipini are olygophagous; only a small number of species are monophagous, especially those trophically related to *Q. cerris* (in the Palaearctic region e.g. *Andricus cydoniae* Giraud, 1959; *A. multiplicatus* Giraud, 1959; *A. grossulariae* Giraud, 1959, and others). Some European forms, for example *Andricus quercuscalicis* (Burgsdorf, 1783) a. f. and *A. hungaricus* (Hartig, 1843) a. f., were found associated with *Q. robur* only. Other host plants (*Q. petraea* and *Q. pubescens*) are also mentioned in the literature for *A. quercuscalicis* (Ambrus, 1974; Ionescu, 1973; Kierych, 1979), however, this data is very dubious and must be confirmed. Several new undescribed leaf- and catkin-galling monophagous *Callirhytis* and *Andricus* species were found in the scrub forest in Florida, on an endemic oak, *Quercus inopina* (Abrahamson *et. al,.* 1998*a*; 1998*b*).

An exception from this rule are heteroecous species, which are transpassing oak section limits and their alternate generations develops on different oak species from different *Quercus* sections (e.g. *Andricus kollari*, *A. quercuscalicis, A. corruptrix* and many others) (Wiebes-Rijks, 1978); see for life cycle Fig. 2: type 3. Oaks can strongly affect life cycles (alternation of generations) of heteroecous cynipid species when one of the oak species involved into the life cycle is absent, although some mechanisms have been recorded in Cynipini to surpass this problem, for example in *Plagiotrochus* (PUJADE-Villar, 1998; Pujade-Villar & Díaz, 2001). However, such phenomenons should be regarded as an exceptional and when one of the host plant species involved into the life cycle of a heteroecous species is absent, than the cynipid species is usually absent too. Otherwords, cynipids distribution depends on host plants distribution. This is the case of all species of the *A. kollari* group, sexual generations of which trophically associated with *Q. cerris.* For example, some cynipid species were detected in Great Britain only after *Q. cerris* was planted in parks in 1735 (Marsden-Jones, 1953) and, thus some species were able to extend their area following their hosts (Marsden-Jones, 1953; Schönrogge *et. al.,* 1994; Stone & Sunnucks, 1992, 1993; Stone, Sunnucks & Schönrogge, 1992). Recently, *A. quercuscalicis* was also registered from the most western part of Ukraine, from the Transcarpathian region (Zerova, Diakontshuk & Ermolenko, 1988; Csóka & Melika, 1993) and from regions right behind the Carpathian Mountains (Zahajkevich, 1954), where *Q. cerris* stands earlier were planted. However, this species is absent further eastward (Zerova, Diakontshuk & Ermolenko, 1988) and even from Crimea (Diakontshuk, 1987) and Moldova (Plugaru, 1963).

It is difficult, not to say impossible, to know with certainty the reasons leading to the appearance of heterogony in gall wasps. According Kinsey (1920, 1922), alternation of generation in Cynipini is only an extreme of stational dimorphism. He based this statement on the similarity of asexual and sexual generations in some cynipid species, for example, in the genus *Neuroterus* Hartig, 1840 (Kinsey, 1920), and on the supposed absence of sexual forms in the group of *Andricus quercuscalifornicus* (Bassett, 1881) in all year calid regions. Thus, according to him, in Southern California alternate forms are absent because of a short time given between emergence of adults and appearance of young galls, while in more northern forms this time interval is longer, he supposed a "normal" alternation of generations (Kinsey, 1922). This hypothesis has not been proved yet, but we must have in mind that in some species, like *A. quadrilineatus* (Folliot, 1964) alternation of generations is not obligated and, thus it further complicates this issue.

On the other hand, Patterson (1928) found non-functional males in the asexual generation of two North-American species, *Neuroterus quercusrileyi* (Bassett, 1880) and *N. contortus* (Weld, 1921), that he interpreted as a remnant of a primitive sexual condition. If we consider this data correct, we could imagine a scenario where a species with two sexual generation, after changing the host plant or tree organ attacked by one of this generations (Cotté, 1926), would produce in one of the generation an asexual form. Such factors are known to greatly affect biology of some species (Pujade-Villar, 1998). Nevertheless, this hypothesis has been normally overlooked because the presence of a parthenogenetic generation is normally considered as a primitive condition within Cynipoidea. Fossil forms are also considered as parthenogenetic, for example, Gerocynipidae, known from Upper Cretaceous (Kovalev, 1995).

Another point we should have in mind is the presence of endosymbiotic bacteria from the genus *Wolbachia* that affect chromosome behaviour of host insect (Stouthamer *et. al.,* 1990). This bacteria cause thelythokous populations (diploid females from non-fertilised eggs and absence or very few rare males) and arrhenothokous populations (males from non-fertilised eggs and females from fertilised ones) in Aylacini and Diplolepidini (Stille, 1984; Plantard, 1997; Plantard *et al.,* 1998, 1999). This fact together with the presence of two annual generations could also explicate the origin of heterogony in cynipids in the past. *Wolbachia* is present in some species of Cynipini (Plantard, *pers. com*.) but according this author although the exact rule of *Wolbachia* in the Cynipini has not been demonstrated and it is possible that it is not related with the parthenogenesis cycle Stone *et al*. (2001); in *Biorhiza pallida*, *Wolbachia* infection, does not interrupt cyclical partenogenesis (Rokas *et al*., 2001).

An interesting question is what is the benefit cynipids have from such a complicate life cycle. One possibility is to avoid parasitoids' pressure by evolving heteroecous life cycle. However, majority of species in both generations have a complex of parasitoids and inquilines which specialized in different gall models. Thus, it is difficult to prove this hypothesis which some authors have named as the "ghost of past-parasitism" (Price & Pschorn-Walcher, 1988; Berdegue *et al*, 1996; Stone & Cook, 1998).

Another interesting point is the variability in emergence period of adults. Since an important part of the population can diapause and remain inside the gall and in this way fluctuations of population are less important and in case of an unfavourable year, an "ex-

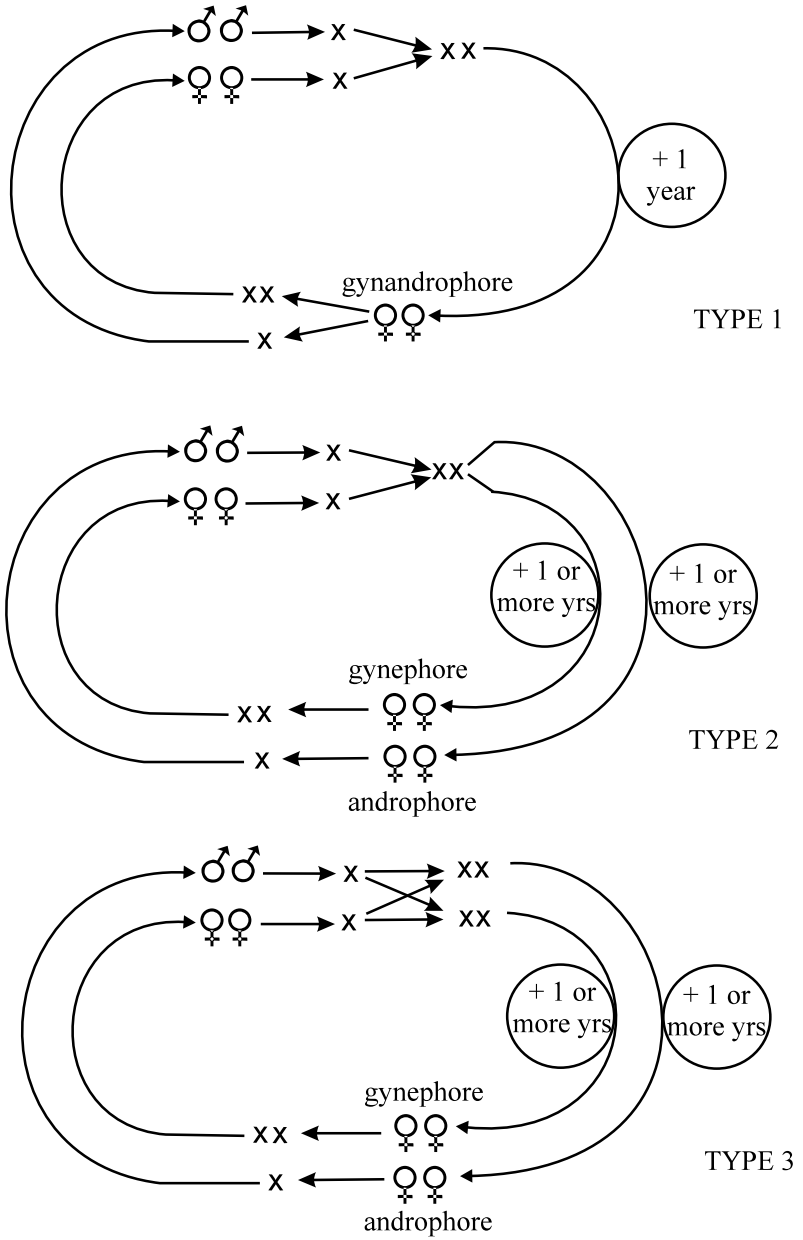

Figure 2. Three types of life cycles in heterogonous gall wasps ASKEW (1984). TYPE 1. *Biorhiza pallida* (part). TYPE 2. *Biorhiza pallida* (part) and *Pediaspis aceris*. TYPE 3. For example, *Andricus quercusradicis*, *A. kollari*, *Neuroterus quercusbaccarum*.

tra" individuals are present in the annual population. This was observed in *A. kollari*, in which a great part of the population remained two years or more inside the galls (Schrönrogge *et. al.,* 1999).

LIFE CYCLE MODEL OF PEDIASPIDINI

According Ronquist (1999) two genera are included into this tribe, *Pediaspis* Tischbein, 1852 and *Himalocynips* Yashimoto, 1970, although the life cycle of *Pediaspis aceris* (Gmelin, 1790) only is known, a species causing galls on different species of *Acer* sp. Sexual galls develop in leaves and asexual ones on roots (= *P. sorbi* Tischbein, 1852), where they can stay in diapause and remain in galls for several years before emerging (Fig. 2: type 2).

Folliot (1964) studied the reproductive model in *Pediaspis* (Fig. 2: type 2). In this life cycle asexual females emerge at the beginning of the year, climb the trunk (since they are apterous) and oviposit into leave buds, originating the sexual generation. Nevertheless, within asexual females we found two different lineages: one which gives exclusively sexual females (known as "gynephores") and another producing only males ("androphores") and, thus the sex is determined in the sexual generation (Fig. 2: type 2). After emergence and copulation, sexual females lay their eggs in mapple roots, which from new asexual females will develop.

LIFE CYCLE MODELS IN CYNIPINI

In Cynipini, biological complexity attains its maximum (Fig. 2). In *Biorhiza pallida* (Olivier, 1791), for example, the life cycle (Fig. 2, types 1 and 2) is very similar to that of *Pediaspis aceris* (Folliot, 1964; Askew, 1984), with an apterous asexual females, developing in subterranean galls on several species of oaks (= *B. aptera* Bosc, 1791) and a sexual form in buds. Here we also have lineages of gynephore females and androphore males, but the life cycle is more complicated, since only some of females are able to produce both females and males (these females are called "gynandrophores"). Assignment of a particular species of Cynipini to a particular model (Fig. 1) is rare, and normally a certain degree of variability can be found in the life cycle of species (Askew, 1984).

In some genera of Cynipini only one of alternate generations is known, like in *Aphelonyx* Mayr, 1881, *Trichagalma* Mayr, 1907*, Zopheroteras* Ashmead, 1897*, Phylloteras* Ashmead, 1897, etc. The absence of an alternation of generations may be merely a reflection of a poor knowledge of the biology of the group. However, in some species a secondary loss of one of the forms have been described. This is the case of *Andricus targionii* Kieffer, 1903, closely related to *A. mukaigawae* and *A. kashiwaphilus*, both being heterogonic species. Abe (1986) exposed that *Andricus targionii* could have lost its sexual form by a mutation of the mechanism which regulates the switch between asexual and sexual generations, isolating this mutant population from the "*A. mukaigawae*" ancestors. This new form would have occupied more northern areas in Japan with a small overlapping zone where both species coexist.

In *Andricus quadrilineatus* another phenomenon takes place. Although this species presents alternation of generations, it is not obliged (Folliot, 1964), and the asexual females can give origin to both asexual and sexual galls. Loss of the sexual generation has also been recorded for *Plagiotrochus suberi* Weld, 1926 *(= P. pardoi* (Nieves-Aldrey, 1985)), species which has loss heterogony after its introduction to the American continent, possibly because of the new pressures it has found in the new environment (Pujade-Villar, 1998; Pujade-Villar & Díaz, 2001). In other species absence of alternate generation might be not secondary, like in *Dryocosmus kuriphilus*, an important pest of chestnut stands in the Eastern Palaearctic, United States and other countries where it has been introduced. In this case the explanation can be double: 1) secondary loss of heterogony, like in *P. suberi*; 2) a primitive feature of the species. It would be interesting to analise all species linked with non-Quercus Fagaceae (*Castanopsis, Castanea*, etc), like *Dryocosmus castanopsidis* (Beutenmueller, 1917), a North American species associated with *Castanopsis chrysophylla* and *C. sempervirens*, known to induce catkin galls in the asexual generation and see if this condition is primitive or it is a secondary loss caused by adaptations to its new hosts.

CURRENT STATE AND FUTURE

The number of cynipid species which for the alternate generations are known is really low (Table 2) in comparison to the number of described species (Table 1). Larger number (over 40 species) of known life cycles can be find in the European fauna. It is even more significant if we relate it to the number of described species in the area. In North America the biology of the same number of species is known, but relatively to the higher diversity of Cynipini, the overall knowledge on the alternation of generations is very poor (near 500 species have been described from North America and north of Mexico (Burks, 1979) and continously new species are described (Melika & Abrahamson, 1997*a*, 1997*b*, 2000*b*). Finally, in some regions the biology of galls wasps is nearly unknown, concomitantly with a scarce knowledge on taxonomy of this fauna, like in Central and South America (Fergusson & Hanson, 1995) or Asia.

It is not easy to close experimentally cynipid life cycles, moreover, in many cases specialists do not known the attacked organ or even host plant, especially in heteroecous species, or in those species which are difficult to rear in experimental conditions and in areas with a high oak diversity, like North America or Mexico, where many times experiments on biology of gall wasps were failed (Melika & Abrahamson, 1997*a*, 1997*b*; Abrahamson *et al*., 1998*a*, 1998*b*).

Another field for more studies are those life cycles which were only supposed but never were experimentally proved. In Table 2 we listed those cynipid species which for the alternation of generations were reasonably recorded. For some species alternate generations were known but never published, like descriptions of different species varieties and their respective counterparts were known but never were published (Kinsey, 1922).

Modern research techniques as the genetic analysis, cladistic studies has been proved that they can be also very useful in identifying alternate generations in cynipids (Stone, *et al*, *pers. com.*; Ronquist, *pers. com*.).

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