Butll. Inst. Cat. Hist. Nat., 71: 83-95. 2003 ISSN: 1133-6889

GEA, FLORA ET FAUNA

The life cycle of *Andricus hispanicus* (Hartig, 1856) n. stat., a sibling species of *A. kollari* (Hartig, 1843) (Hymenoptera: Cynipidae)

Juli Pujade-Villar*, Roger Folliot** & David Bellido*

Rebut: 28.07.03
Acceptat: 01.12.03

Abstract

The marble gallwasp, *Andricus kollari*, common and widespread in the Western Palaeartic, is known for the conspicuous globular galls caused by the asexual generations on the buds of several oak species. The sexual form known hitherto, formerly named *Andricus circulans,* makes small gregarious galls on the buds of Turkey oak, *Quercus cerris*; this oak, however, is absent from the Iberian Peninsula, where on the other hand the cork oak, *Q. suber,* is present. Recent genetic studies show the presence of two different populations or races with distribution patterns similar to those of *Q. cerris* and *Q. suber*. We present new biological and morphological evidence supporting the presence of a sibling species of *A. kollari* in the western part of its range (the Iberian Peninsula, southern France and North Africa), *Andricus hispanicus* n. stat.. Biological and morphological differences separating these two species from other closely related ones are given and the new sexual form is described for the first time. This form of *A. hispanicus*, causing isolated bud galls in *Q. suber,* is identical to *Andricus mayeti* n. syn. and *Andricus niger* n. syn. and so we consider *A. mayeti* and *A. niger* to be junior synonyms of *A. hispanicus*. Finally, possible causes of the speciation of *A. kollari* and *A. hispanicus* are discussed.

KEY WORDS: Cynipidae, *Andricus*, *A. kollari, A. hispanicus*, biological cycle, sibling species, sexual form, speciation, distribution, morphology, *A. mayeti*, *A. burgundus*.

Resum

Cicle biològic d'*Andricus hispanicus* (Hartig, 1856) una espècie bessona d'*A. kollari* (Hartig, 1843) (Hymenoptera: Cynipidae)

Andricus kollari és una espècie molt comuna distribuida a l'oest del paleartic coneguda per la gal·la globular i relativament gran de la generació assexual que es localitza als borrons de diverses espècies de roure. La forma sexual coneguda fins avui, denominada *Andricus circulans*, provoca petites gal·les gregaries als borrons del roure turc *Quercus cerris*, (aquest roure no es troba a la península Ibèrica, on si que hi ha *Q. suber*). Recents estudis genètics mostren la presència de dues poblacions o races diferents amb un patró de distribució similar al de *Quercus cerris* i al de *Q. suber*. En aquest estudi presentem evidències bio-

---

* Universitat de Barcelona. Facultat de Biologia. Departament de Biologia Animal. Avda Diagonal 645. E-08028 Barcelona, Spain. E-mail: pujade@porthos.bio.ub.es
** Université de Rennes 1. Faculté Sciences. C.N.R.S. UPRES- A 6026. Équipe Canaux Récepteurs Membranaires. Bât 13-Campus de Baulieu. 35042-Rennes Cedex - France.

lògiques i morfològiques que posen de manifest la presència d'una espècie bessona d'*Andricus kollari* en la zona oest d'Europa (península Ibèrica, sud de França i nord d'Àfrica), *Andricus hispanica* status n. Es descriuen les diferències biològiques i morfològiques que permetran separar aquestes dues espècies d'altres espècies molt properes, i es descriu per primer cop la forma sexuada d'*Andricus hispanica* que ocasiona gal·les aïllades als borrons de *Quercus suber*. Aquesta forma és idèntica a *Andricus mayeti* (= *Andricus niger* syn. n.), així doncs considerem *Andricus mayeti* com a nova sinonimia d'*Andricus hispanica*. Per acabar, es discuteixen les raons que van poder ocasionar la separació específica d'*Andricus kollari* i *A. hispanica*.

MOTS CLAU: Cynipidae, *Andricus*, *A. kollari, A. hispanicus*, cicle biològic, espècies bessones, forma sexual, especiació, distribució, morfologia, *A. mayeti*, *A. burgundus*.

Resumen

Ciclo biológico de *Andricus hispanicus* (Hartig, 1856) una especie gemela de *A. kollari* (Hartig, 1843) (Hymenoptera: Cynipidae)

Andricus kollari, es una especie muy común distribuida en el oeste del paleártico, conocida por la agalla globular y relativamente grande de la generación asexual producida en yemas de varias especies de roble. La forma sexual conocida hasta hoy, denominada *Andricus circulans*, provoca pequeñas agallas gregarias en yemas del roble turco *Quercus cerris*, (este roble no se encuentra en la Península Ibérica, donde si hay *Q. suber*). Recientes estudios genéticos mostraron la presencia de dos poblaciones o razas distintas con un patrón de distribución similar al de *Quercus cerris* y al de *Q. suber*. En este estudio presentamos evidencias biológicas y morfológicas que ponen de manifiesto la presencia de una especie gemela de *Andricus kollari* en la zona oeste de Europa (Península Ibérica, parte sur de Francia y Norte de África), *Andricus hispanica* status n. Se describen estas diferencias biológicas y morfológicas que permitirán separar estas dos especies de otras especies muy cercanas, y se describe por primera vez la forma sexual de *Andricus hispanica*, que ocasiona agallas aisladas en las yemas de *Quercus suber*. Esta forma es idéntica a *Andricus mayeti* (= *Andricus niger* syn. n.), así pues consideramos *Andricus mayeti* como nueva sinonimia de *Andricus hispanica*. Para finalizar, se discuten las razones que pudieron ocasionar la separación específica entre *Andricus kollari* y *A. hispanica*.

PALABRAS CLAVE: Cynipidae, *Andricus*, *A. kollari, A. hispanicus*, ciclo biológico, especies gemelas, forma sexual, especiación, distribución, morfologia, *A. mayeti*, *A. burgundus*.

Introduction

The marble gall wasp, *Andricus kollari*, is one of the best known cynipids and has received great attention in the literature because of its interesting and complex life cycle and conspicuous unisexual galls. In former times these galls were collected for industrial purposes for their high tannin content. The dry substance can consist of up to 65 % tannins, and this substance was used for tanning leather or producing ink (Kieffer, 1897-1901). The native range of the species is divided geographically between south-western Europe (mostly the Iberian Peninsula) and eastern Europe, although human introduction of the host of the sexual generation, *Quercus cerris* (Turkey oak), has favoured its dispersal over northern and north-western Europe (Schönrogge *et al.*, 1998), where it is now one of the most easily found species at many sites.

Beijerinck (1902) described the life cycle of this species, and later Marsden-Jones (1953) and Folliot (1964) confirmed it. There is a conspicuous unisexual generation forming spherical monolocular bud galls (10-30 mm in diameter) on various species of *Quercus* subgenus *Quercus* while the bisexual generation forms small gregarious galls in buds of *Q. cerris*. Some authors have proposed that *A. kollari* might reproduce without a sexual generation in its lifecycle in regions where *Q.*

cerris is either rare (such as the Transcarpathian region of the Ukraine: Melika & Csóka, 1993; Csóka, 1997) or entirely absent (Iberia: Nieves-Aldrey, 1987; Csóka *et al.*, 1998; Dajoz, 1999). Pujade-Villar (1992) reported the presence of a sexual generation in Iberian populations, although it was not described because only the sexual female was found.

Recent genetic results using allozyme data (Stone *et al.*, 2001) support the presence of a sexual generation in Iberian populations and suggest a genetic isolation between the eastern and western populations. According to the results the eastern and western forms of *A. kollari* would have differentiated completely between 1 and 2 million years ago and have to be considered separate species. The western form is found in the Iberian Peninsula, extending into south-west France, while the eastern form occurs in eastern Europe, including the Italian and Balkan peninsulas, as well as in north and north-western Europe. It is very interesting that the distribution of this western form shows a close coincidence with the distribution of *Q. suber* (cork oak), an oak closely related to *Q. cerris*.

The present study describes the discovery of the sexual male of the Iberian form and the identification of the host of the sexual generation as *Q. suber*, so that the redescription of the western form of *A. kollari* as a new species can now be made.

Material and methods

Two sexual females of *Andricus* were found ovipositing in buds of *Q. pubescens* on Montseny in the north-east of the Iberian Peninsula on 18th April 1987. The branch where the females were found was kept inside a sleeve until July 1987; the galls obtained (one for each sexual female) were beyond doubt of the *A. kollari* type, and the adults obtained confirmed this observation. This experiment has been mentioned previously in Pujade-Villar (1992) and showed that although *Q. cerris* is absent from the Iberian Peninsula, the so-called Iberian *A. kollari* have an alternating life cycle in this area. As mentioned in Pujade-Villar (1991), this sexual form is slightly different from the sexual form of eastern *A. kollari* (formerly called *A. circulans*); the relationship between the agamic form (*A. kollari*) and the sexual form (*A. circulans*) was established by experimental studies by Benson (1953). The two specimens from Montseny mentioned above were compared with: a) adults emerged from sexual galls found on *Q. suber* attributed to *A. mayeti*; b) a series of adults reared from them, because of their high similarity; c) sexual galls of eastern *A. kollari* obtained experimentally by R.F. in the north of France. Finally it was also compared with other sexual forms of the *kollari* group (see Folliot *et al.*, 2003).

Biological experiments with both Spanish and Northern French populations were also carried out over several years. A large number of unisexual galls collected in Spain and supposedly linked to *Q. suber* were brought to France, where unisexual females were reared for experiments on *Q. cerris* (R.F.), while northern French unisexual galls were taken to Spain, where experiments on *Q. suber* were performed (J. P.-V.).

We follow the current terminology of morphological structures (Gibson, 1985; Ronquist & Nordlander, 1989), surface sculpturing is given after Harris (1978). Measurements and abbreviations used here include: POD (post-ocellar distance) is the distance between the inner margins of the posterior ocelli; OOD (ocellar-ocular distance) is the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; COD is the distance between lateral and frontal (central) ocellus.

Results

Two sexual females of *Andricus* were found ovipositing on *Q. pubescens* and the branch was kept in a sleeve. The agamic generation that developed turned out to be *A. kollari* (Pujade-Villar, 1992). These females of the sexual form of Iberian *A. kollari* were morphologically identical to adults obtained from *A. mayeti* galls on *Q. suber*, except for minor differences falling within the range of intraspecific variation.

The ephemeral and inconspicuous bud galls of *A. mayeti* on *Q. suber* are normally isolated or in pairs; sexual adults are of a black colour with a striated mesopleuron, but with several clear morphological and biological differences from the sexual form of eastern *A. kollari*.

Biological experiments showed that whereas unisexual females from Brittany (now known to be of eastern origin) quickly inspected and oviposited into buds of *Q. cerris*, they showed no interest in *Q. suber*. Unisexual females of *A. kollari* collected in Spain showed the reverse behaviour: when left on *Q. cerris* branches they showed no interest in them and died before laying any eggs on the wrong host, while on *Q. suber* they showed an active oviposition behaviour. Despite the large number of unisexual females observed, oviposition on the wrong host only exceptionally occurred and no galls developed in these cases (R.F.). In any case, this oviposition into an oak species other than the usual host can be induced at a low rate in the laboratory when females are given no choice, although no galls were observed to develop in such cases (e.g. the oviposition of the sexual form of *A. kollari* on *Q. robur* (Marsden-Jones, 1953) or on *Q. ilex, Q. pubescens* and *Q. robur* (Folliot, 1964); the latter author also reported the sexual form of *A. kollari* ovipositing on *Q. ilex*, but no agamic galls were ever found).

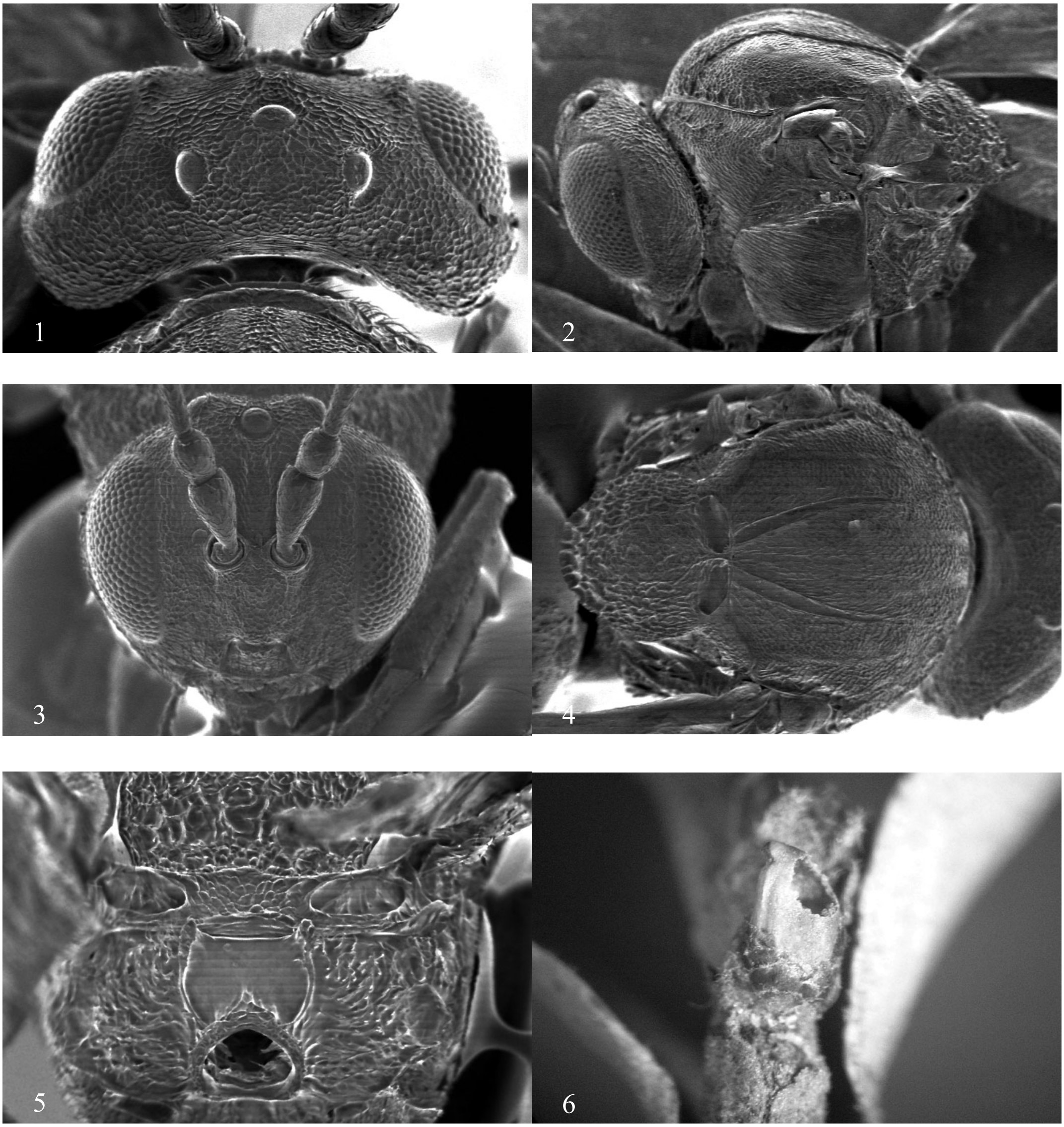
Thus it would appear that the sexual form of western *A. kollari* is *A. mayeti,* and a description of the new species can now be made. This should be called *Andricus hispanicus* (Hartig, 1856) n. stat., since it was Hartig who first described galls of *A. kollari* from the south of Spain (in the Sierra de Ronda) and thus inside the Iberian native range (Pujade-Villar & Bellido, 2000). Considering *A. circulans* to be the sexual form of *A. hispanicus* (i. e. Iberian *Andricus kollari*) as Nieves-Aldrey (2001) does is mistaken (Pujade-Villar, 1991; 1992; 1997), especially when *Q. cerris* is not found in the Iberian Peninsula; a new sexual form for *A. hispanicus* needs to be described.

Andricus hispanicus (Hartig, 1856) n. stat.
Cynips hispanica Hartig, 1856. Agamic gall
Cynips kollari var *minor* Kieffer, 1897-1901. Agamic form
Cynips kollari minor (Kieffer) Dalla Torre & Kieffer, 1910 (syn. in Bellido, Ros-Farré, Melika & Pujade-Villar, 2003)
Andricus hispanica (Hartig) Pujade-Villar & Bellido, 2000 after Benson, 1953.
Andricus mayeti Kieffer, 1896. *Bull. Soc. Entomol., France*: 370 (sexual female and gall) n. syn.
Andricus luteicornis var *niger* Kieffer, 1901. *Ann. Soc. Entom. France*, 70: 453 (sexual gall) n. syn.
Andricus l. var *niger* Tavares, 1902 *Brotéria*, 1: 104 (male, female and gall); homonymy with Kieffer, 1901 n. syn.
Andricus niger Tavares, 1916. *Brotéria Sér zool.*, 14: 84 n. syn.

Redescription of the sexual form

Type material: The type material from the Kieffer collection has been lost.

Material studied– Experimental material: 2



FIGURES 1-6. Morphological aspects of the sexual form of *Andricus hispanicus* (*A. mayeti*). Head in dorsal view (1), head and mesosoma in lateral view (2), head in frontal view (3), mesosoma in dorsal view (4), propodeal area (5) and gall (6).

females ovipositing on *Quercus pubescens*; 7 males and 12 females obtained from galls collected in several localities of the province of Barcelona (north-east Spain). All material deposited at Barcelona University.

Length: 1.7-2.0 mm (for males and females).
Colour– All the body black. Wing veins dark brown. Some specimens with brown antennae, instead of black.
Female head (Figs 1, 3): Without pubescence;

in dorsal view around 2.09-2.36 times as wide as long and in frontal view 1.13 times as high as wide. Genae coriaceous-alutaceous, not broadened behind compound eyes. POD twice OOD; OOD 1.4 times lateral ocellus diameter and more or less equal to COD (ratio POD:OOD:COD:lateral ocellus diameter is 22:10:10:7). Coriaceous-alutaceous sculpture. Clypeus conspicuous and suboval in shape. Face with only some very short and weak irradiating striae around clypeus, never reaching either antennal toruli or compound eye margin. Transfacial line more or less equal to eye height. Diameter of toruli more or less 1.5 times their separation and slightly longer than distance between toruli and eye margin. Antenna with 13 segments, 0.8 times as long as body or slightly longer; pedicel 2.0 times as long as wide; first flagellomere 1.2 times as long as the second and 1.6 times as long as the pedicel; subsequent flagellomeres gradually decreasing in length, later flagellomeres longer than wide and the last more or less twice as long as wide.

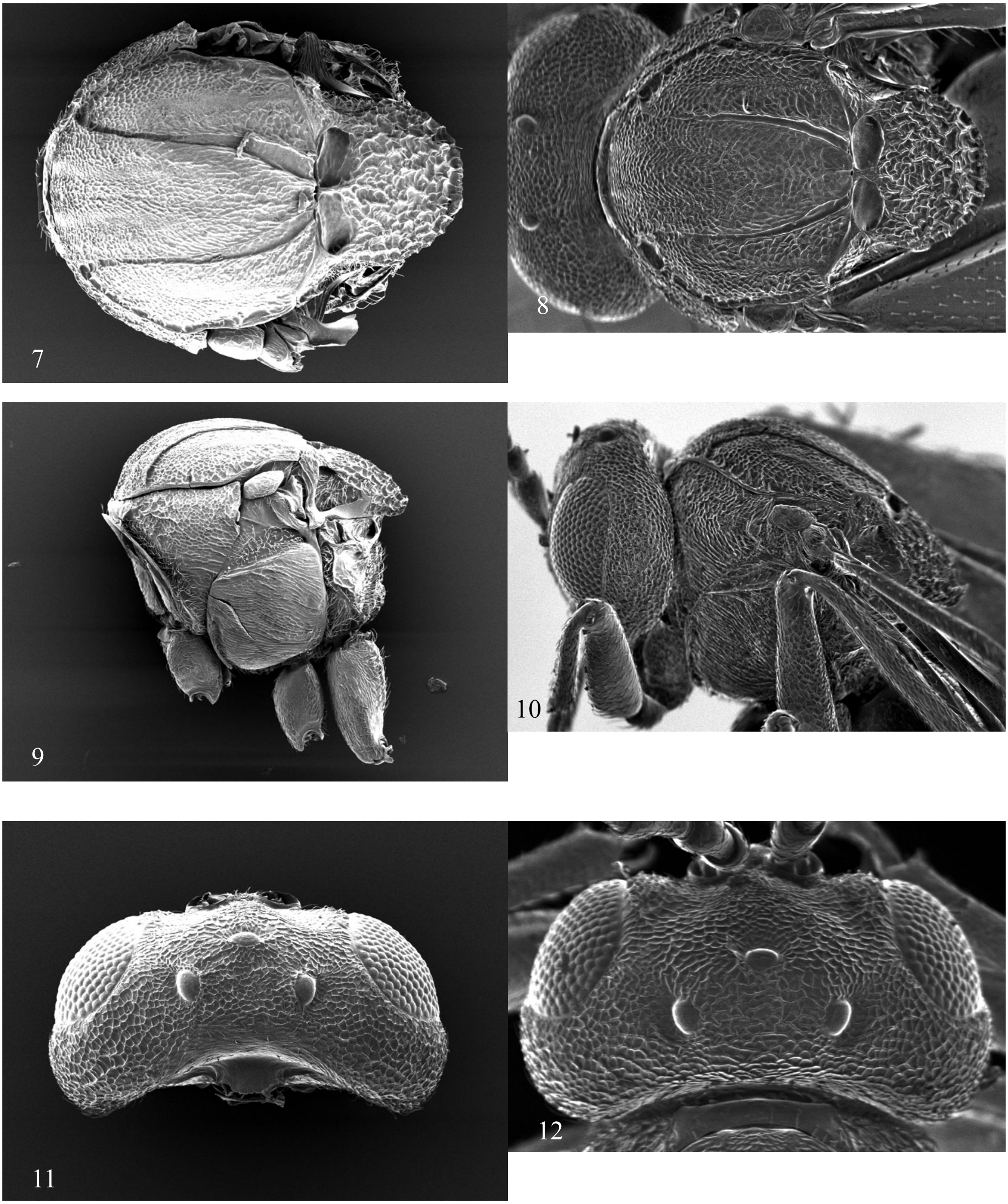
Female mesosoma (Figs 2-5): Without pubescence except for some hairy zones on the propodeum, with coriaceous-alutaceous sculpture. Notauli complete, anteriorly less impressed, posteriorly convergent and wide, delimiting an area with regular closely reticulate-alutaceous sculpture and not longitudinally striated. Median scutal line absent. Mesopleuron completely striated, with some striation also on lateral inferior margin of pronotum. Circular scutellum, only slightly wider than long, with weak reticulated sculpture, less evident in the central part usually delimited by two divergent carinae, marginated laterally and not lobed posteriorly. Scutellar foveae oval, disposed transversely, smooth, shiny and not pubescent inside, not delimited posteriorly by a carina and separated from each other by a septum. Metanotal foveae elongated and interiorly pubescent. Metascutellum sculptured. Lateral carinae of propodeum thin, of a uniform thickness, only slightly bowed outwards, internal area smooth and shiny (a weak median carina is present in the lower part of the propodeal area). Wings hyaline. Forewing margin with short and scattered setae on its anterior margin; radial cell 5.0 times as long as broad; 2r vein angled. Areolet normally conspicuous. Tarsal claws with an acute basal lobe and forming an acute angle. Anterior tibiae provided with only a few short and applied hairs.

Female metasoma: Slightly shorter than head plus mesosoma together; without pubescence except at the base of the 2nd metasomal tergite. Ventral spine of hypopygium around 3 times longer than broad, with sparse setae not forming an apical tuft; when the adult is dried this relative length of hypopygial spine is lower (around 1-2 times) because both valves open longitudinally.

Male: Same as female, but antenna with 14 segments, the third one curved, dorsally flattened, proximally excavate and distally expanded, and with weaker sculpture, more alutaceous.

Distribution: Iberian Peninsula, southern France, but probably also in North Africa, always near to its host, *Quercus suber*. The Corsican record (Pujade-Villar *et al*., 2000) must be regarded as provisional because the agamic form was not collected (Villeman *pers. comm.*); the agamic gall was not found although is very easy to detect.

Gall (Fig. 6): Similar to other sexual galls of the *Andricus kollari* group. A small bud gall (1.5 × 1.2 mm) on *Quercus suber*, isolated or in pairs (unlike those of *A. circulans* or *A. larshemi*), with its basal part hidden from view by bud-scales and apical part (covering 1/3 to 1/2 of the gall) projecting outside. The surface of the gall is of a yellowish to brown colour, nearly smooth, with no striation,



FIGURES 7-12. Morphological aspects of the sexual form of *Andricus kollari* sensu stricto (*A. circulans*) (7, 9, 11) and *A. burgundus* (8, 10, 12). Mesosoma in dorsal view (7-8) and in lateral view (9-10). Head in dorsal view (11-12). (Figures 7, 9 and 11 are also available at http://morphbank.ebc.uu.se, as well as other images.)

without pubescence; the gall is ovoid and more or less conical, the tops are pointed, and the gall wall is very thin. Galls appear in March or April and adults emerge shortly afterwards through a large round lateral opening below the top.

Taxonomic comments: Kieffer (1901) described galls of *Andricus luteicornis* var *niger* from information given by Tavares. Tavares (1902) described the male and redescribed the gall of this variety, entering inadvertently into homonymy with Kieffer's name. Later on Tavares (1916) considered the variety to be a different species. *A. niger* has been recorded from Portugal and Spain (Nieves-Aldrey, 2001) and from Corsica (Pujade-Villar *et al*., 2000), although in retrospect this latter reference must be treated with caution. The descriptions of the galls and adults of *A. mayeti* Kieffer and *A. niger* are identical (Pujade-Villar, 2002), as are the distributions of the two species. The only difference is in the relative length of the hypopygial spine (Kieffer, 1897-1901: 397 & 420; Kieffer, 1902: 559), but this difference falls within the range of intraspecific variation. Therefore we consider *A. niger* Kieffer, 1901, to be a new synonym of *A. mayeti* Kieffer, 1896 and thus also of *A. hispanicus*.

The sexual form of *A. hispanicus* (*A. mayeti*) is very close morphologically to the sexual form of *A. kollari* (*A. circulans*) and to *A. burgundus* Giraud, 1859, only known in its sexual form. All of them have a longitudinally striated mesopleuron, the posterior margin of the scutellum rounded and a reticulated-alutaceous sculpture on the scutum.

The sexual form of *A. hispanicus* differs from the sexual form of *A. kollari* in the form of the notaulus, which is wider and very conspicuous in *A. kollari* and shallower anteriorly and narrower in *A. hispanicus* (Figs. 7 and 4, respectively); in the scutellum sculpture, rougher in *A. kollari* than in *A. hispanicus* (Figs. 7 and 4, respectively); in the shape of the scutellum, oval and convex in *A. kollari*, rounded and less convex in *A. hispanicus* (Figs. 7 & 11 and 4 & 2, respectively); and in the galls (in groups on *Quercus cerris* in *A. kollari* and isolated or in pairs on *Q. suber* in *A. hispanicus*).

However, in the unisexual generation the adults and the galls of the two species are impossible to separate morphologically (Bellido *et al*., 2003). Certainly other species in the *A. kollari* group are very similar morphologically and for a long time many of the unisexual adults of the species of this group were impossible to separate (Kieffer, 1897-1901; Dalla Torre & Kieffer, 1910; Tavares, 1931) but the galls are very different. The case of the western and eastern forms of *A. kollari* sensu lato is somewhat different, since no morphological differences can be found and moreover the galls are identical. Thus *A. hispanicus* and *A. kollari* must be considered sibling species that can only be separated by biology and by the sexual adults and their galls.

As regards other previously described sexual forms in the *A. kollari* group (Docters van Leeuwen, 1956; Docters van Leeuwen & Dekhuijzen-Maasland, 1958; Wiebes-Rijks, 1978), the sexual form of *A. hispanicus* is clearly different from all of them, either in the galls or in morphological characters mainly relating to the mesosoma sculpture and notauli. Galls and adults of the sexual form recently described for *A. corruptrix* and the sexual form of *A. hispanicus* are similar but show some clear differences such as the propodeal area and notauli (see Folliot *et al*., in press).

A. hispanicus is also very close morphologically to *A. burgundus*, recently redescribed by Nieves-Aldrey (2001). However the characters given by this author are not satisfactory for separating the two species. *A.*

burgundus has narrow notauli clearly separated at their base (Fig. 8), while *A. hispanicus* has wider and posteriorly convergent notauli (Fig. 4), like *A. kollari* (Fig. 7). Moreover, the scutellum and scutum sculpture is strongly rugose in *A. burgundus* (Fig. 8), a character also present in *A. kollari* (Fig. 7), while in *A. hispanicus* the sculpture is much weaker (Fig. 4); the ocelli are smaller in *A. hispanicus*; the ratio of OOD to the ocelli diameter is bigger in *A. burgundus* (Fig. 1, 12); and the sculpture on the dorsal part of the head and the lateral part of the thorax is weaker in *A. hispanicus* (Fig. 1, 2) than in the other two species (Figs 9-12). The propodeal carinae in these three species are very similar, parallel or curved slightly outwards, and cannot be used as diagnostic characters as they can with other species of *Andricus*; finally, all three species often show signs of a weak median propodeal carina.

Discussion

The results of our biological experiments clearly show the lack of recognition of *Q. cerris* by agamic females of *A. hispanicus*. As Stone *et al.* (2001) suggest, a divergence in the chemical cues associated with oviposition behaviour may have evolved between *A. hispanicus* and *A. kollari* sensu stricto.

Genetic results also support the presence of two clearly differentiated geographical genotypes within *A. kollari* sensu lato, closely corresponding to the distributions of their respective sexual form hosts; there was very little evidence of gene flow (Stone *et al.*, 2001). This is also supported by our own observations, since galls of the sexual generation are found in great numbers locally, facilitating mating between males and females. After mating, dispersal of females probably takes place, since unisexual galls could be found in places very far from *Q. suber* stands. The agamic form, which is bigger, would have a greater ability to disperse and because of its superior flight capacity would be able to locate *Q. suber*, the host of the sexual generation, in spite of the discontinuous distribution of this oak in the Iberian Peninsula (Toumi & Lumaret, 1998).

But what was the origin of *A. hispanicus*? Sequence data suggest that the Iberian population of *A. kollari* sensu lato began to diverge from the Central European and Balkan populations 2-4 million years ago, through a host shift of the sexual generation between *Q. cerris* and *Q. suber* (probably from *Q. cerris* to *Q. suber*) (Stone *et al.*, 2001; Stone, *pers. comm.*). The question is how this shift took place.

Some authors state that host shifts have been rare, especially in the Cynipini because of their extreme specialisation and low dispersal abilities (Cornell & Washburn, 1979; Kinsey, 1920), and Cynipini are certainly constrained by the need to successfully induce galls (Abe, 1988, 1991, 1998; Cook *et al.*, 1998, 2002). However some recent host shifts from wild to domestic roses are known amongst Nearctic *Diplolepis* (Tribe Rhoditini) (Shorthouse, 1988, 1994; Shorthouse & Brooks, 1998) and some authors (Stone *et al.*, 2001) propose that host shifts to *Quercus* subgenus *Cerris* from *Quercus* subgenus *Quercus* must have occurred. Host shifts may also occur (or be favoured) as a result of strong selection pressures, such as intraspecific competition or parasitism. This has been proposed as the mechanism generating two host races of the gall-inducing tephritid fly *Eurosta solidaginis* (Hess *et al.*, 1996; Feder, 1995). However, although parasitoid pressure plays an important role in cynipid population dynamics (Washburn & Cornell, 1981; Frankie & Morgan, 1984; Sitch *et al.*, 1988; Plantard *et al.*, 1996), given the similarity of the galls it seems unlikely that parasitoid-induced pressure would play the major role in this case. In the case of *A. kollari* and *A. hispanicus* it is hard to test this hypothesis, although gall similarity and the rapid shift of parasitoids from native galls to invasive species of cynipids make the hypothesis unlikely.

The present distribution of the two sibling species is explained by the glacial and post-glacial movements of flora and fauna taking place in the Western Palaearctic during the Pleistocene (Stone *et al.*, 2001). In Europe, mountain ranges hindered the retreat of the Arcto-Tertiary forests, which were devastated by the cold conditions, so that only some genera survived, oaks amongst them (Collinson, 1988; Sitte *et al.*, 1994). Indeed, a very rapid onset of cold conditions, such as seems to have occurred at times, would have allowed no time for the flora to retreat and isolation would have quickly occurred, whether there were mountain ranges in the way or not. Oak diversity was greatly reduced, and probably gall wasp diversity as well, since the Tertiary oak flora was rich and many species were abundant (Mai, 1995). European cynipid populations were greatly affected by the repeated glaciations, since they were confined by the ice sheets, together with their hosts, to refuges mainly in the Italian, Balkan and Iberian peninsulas but also in North Africa and the Eastern Mediterranean (Collinson, 1988; Roberts, 1989; Delcourt & Delcourt, 1988; Bennett *et al.*, 1991; Hewitt, 1996). Present patterns were established mainly after the recolonisation of previously iced regions. In Europe, recolonisation from both the east and the west reunited the oak flora, except for those oaks remaining in their glacial refuges, like *Q. faginea* in the Iberian Peninsula and *Q. cerris*, because of its narrower climatic tolerance (Sandor, *pers. comm.*), in Eastern Europe. The colonisation of Central Europe took place from both eastern and western refuges as the presence of a mixed region of eastern and western oak genotypes in Central Europe suggests (Ferris *et al.*, 1993).

Evergreen oaks and other Mediterranean flora suffered an even greater restriction in their distribution, and were reduced to some localities in the south of the Iberian Peninsula, the Eastern Mediterranean and North Africa (Roberts, 1989), mainly in suitable microclimates in the mountains (Willis, 1992, 1994). The conditions in these refuges were different for each refuge; the Balkans are especially complicated because of their topography, which creates a wide range of environmental variation (Willis, 1994). *Quercus cerris* and Iberian *Q. suber* would have been isolated from each other increasingly often as interglacials got cooler. Iberian *Q. suber* and *Q. cerris* are not now in contact naturally even under interglacial conditions; the contact is an indirect one through Italian *Q. suber*, which is rather different as Toumi & Lumaret (1998) show. Geology is another factor limiting the spread of *Q. suber*, since calcareous soils would have been a barrier to it and may have helped to isolate the Iberian and Italian populations from one another.

Thus recolonisation movements of the oak hosts from glacial refuges would explain the present distribution pattern of the two gall wasp species; *Andricus hispanicus* would have reinvaded southern France from its Iberian refuges and *A. kollari* sensu stricto from Balkan and Italian ones. In Italy, although genetic analyses have not detected *A. hispanicus*, since the samples were collected in zones without *Q. suber*, the presence of this species may yet be confirmed after the recent discovery of galls apparently belonging to *A. niger*, now shown to be the sexual generation of *A. hispanicus*, in Corsica (Pujade-Villar *et al.*, 2000), although this record must be considered provisional until more studies are carried out. If this record is confirmed, it will imply that *A. hispanicus* has spread together with its host and probably has the same distribution range, although the inconspicuousness of the sexual galls and their similarity to those of *A. kollari* sensu stricto mean that the species remains undetected in many places. It would be interesting to carry out further genetic analyses of unisexual adults in the contact zones where both *Q. suber* and *Q. cerris* are present, to test whether both species are present.

However, the separation of the two species seems to be older than the last glaciation, and although the glaciations were not so intense 2-4 million years ago (Webb & Bartlein, 1992), the presence of significant ice sheets at that time suggests that they probably played some role in the speciation of the two lineages.

Recent studies on allozyme variation in *Q. suber* and current DNA-based studies at the University of Cambridge (John Parker, *pers. comm.*) show that the Iberian Peninsula is probably the centre of origin of the species and supports a higher genetic diversity, and that, as the paleobotanical data corroborate, several cork oak migrations to North Africa, south-eastern France and Italy have taken place since the end of the Tertiary (Toumi & Lumaret, 1998). On the basis of this data, the origin of *A. hispanicus* may be explained through a host shift favoured by a closer proximity of *Q. suber* to *Q. cerris* than at present and a subsequent geographical isolation caused by cold periods. The Iberian origin of *Q. suber* suggests that the origin of *A. hispanicus* probably lies in the Iberian Peninsula, and subsequent glaciations would make the Iberian Peninsula and North Africa perfect refuges for this species.

Other species of *Andricus* may be similar cases to *Andricus kollari* sensu lato, since their distributions include a great part of the Western Palaearctic, both in zones where *Q. cerris* or other closely related oaks are present (e.g. Eastern Europe and Turkey) and in zones where the most likely host of the sexual generation is *Q. suber* (Atkinson, 2000; Melika *et al*., 2000: Nieves-Aldrey, 2001; Cook *et al*., 2002; Rokas *et al*., 2003). However, each case must be studied carefully and genetic, biological and morphological studies must be carried out. Recent genetic studies show different lineages of *A. quercustozae* for each oak glacial refuge, and in this case the Iberian lineage has diverged from other Western Palaearctic populations and only shows a subset of the ancestral allozyme polymorphism (Rokas *et al*., 2003).

Acknowledgements

We would especially like to thank Palmira Ros i Farré (University of Barcelona) for the SEM pictures illustrating this paper and Graham Stone for his valuable comments about the genetic data.

Bibliography

ABE, Y. 1988. Two host races in *Andricus mukaigawae* (Mukaigawa) (Hymenoptera: Cynipidae). *Appl. Ent. Zool*., 23(4): 381-387.

ABE, Y. 1991. Host race formation in the gall wasp *Andricus mukaigawae*. Entomol. Exp. Appl., 58: 15-20.

ABE, Y. 1998. Karyotype differences and speciation in the gall wasp *Andricus mukaigawae* (s. lat.) (Hymenoptera: Cynipidae), with description of the new species *A. kashiwaphilus*. *Ent. Scand*., 29: 131-135.

ATKINSON, R. J. 2000. The genetic analysis of natural history, reproductive strategy and population structure in European oak gallwasps (Hymenoptera: Cynipidae). PhD Thesis. University of Oxford.

BEIJERINCK, M. W. 1902. Ueber die sexuelle Generation von *Cynips kollari*. *Marcellia*, 1: 13-18.

BELLIDO, D.; ROS-FARRÉ, P.; MELIKA, G & PUJADE-VILLAR, J. 2003. Review of the asexual forms of *Andricus kollari* species-group (Hymenoptera:

Cynipidae, Cynipini). *Annales Historica Naturalis Musei Hungarici*, 64: 171-222.

BENNETT, K. D.; TZEDAKIS, P. C. & WILLIS, K. J. 1991. Quaternary refugia of north European trees. *Journal of Biogeography*, 18: 103-115.

BENSON, R. B. 1953. Revision of nomenclature. In: Marsden Jones, E., *A study of the life cycle of* Adleria kollari *Hartig the marble or Devonshire gall. Trans. R. Ent. Soc. London.,* 104: 220

COLLINSON, A. S. 1988. *Introduction to world vegetation*. 2nd Ed. Unwin & Hyman.

COOK, J. M.; STONE, G. N. & ROWE, A. 1998. Patterns in the evolution of gall structure and life cycles in oak gall wasps (Hymenoptera: Cynipidae). In: Csóka, G; Mattson, W. J.; Stone, G. N. & Price, P. W. (eds.). *The Biology of Gall-Inducing Arthropods*. pp. 261-279. North Ctral. Res. Station. Forest Service, U.S. Dept. of Agric. Minnesota.

COOK, J. M.; ROKAS, A.; PAGEL, M. & STONE, G. N. 2002. Evolutionary shifts between host oak species and host plant organs in *Andricus* gallwasps. *Evolution*, 56: 1821-1830.

CORNELL, H. V. & WASHBURN, J. O. 1979. Evolution of the richness-area correlation for cynipid gall wasps on oak trees: a comparison of two geographic areas. *Evolution*, 33(1): 257-274.

CSÓKA. G. 1997. *Plant galls*. Agroinfrom publishing. Budapest, Hungary.

CSÓKA. G., STONE, G. N., ATKINSON, R. & SCHÖNROGGE, K. 1998. The population genetics of postglacial invasions of northern Europe by cynipid gall wasps (Hymenoptera: Cynipidae). In: *The Biology of Gall-Inducing Arthropods*. Csóka, G., Mattson, W. J., Stone G. & Price, P. W. (Eds.). Proceedings of the international symposium; 1997 August 14-19; Mátrafüred, Hungary. Gen. Tech. Rep. NC-199. St. Paul, MN: USA. Department of Agriculture, Forest Service, North Central Research Station: 280-294.

DAJOZ, R. 1999. *Entomología forestal*. Ed. Mundi-Prensa, Madrid. 548 pp.

DALLA TORRE, C. W. & KIEFFER, J. J. 1910. *Cynipidae. Das Tierreich*, 24. Berlin: 891 pp. +35 pl.

DELCOURT, P. A. & DELCOURT, H. R. 1988. Quaternary landscape ecology: relevant scales in space and time. *Landscape Ecology*, 2(1): 23-44.

DOCTERS VAN LEEUWEN, W. M. 1956. The bigamic generations of *Andricus corruptrix* Schlechtendal and *Andricus lignicolus* Hartig (Hymenoptera, Cynipidae). *Tijdschr. Ent*., 98: 251-256.

DOCTERS VAN LEEUWEN, W. M. & DEKHUIJZEN-MAASLAND, J. M. 1958. The bigamic generations of *Andricus corruptrix* Schlechtendal and *Andricus lignicolus* Hartig (Hymenoptera, Cynipidae). Part II. *Tijdschr. Ent*., 101: 101-111.

FEDER, J. L. 1995. The effects of parasitoids on sympatric host races of *Rhagoletis pomonella* (Diptera: Tephritidae). *Ecology*, 76: 801-813.

FERRIS, C., OLIVER, R. P., DAVY, A. J. & HEWITT, G.M. 1993. Native oak chloroplasts reveal an ancient divide across Europe. *Molecular Ecology*, 2, 337-344.

FRANKIE, G. W. & MORGAN, D. L. 1984. Role of the host plant and parasites in regulating insect herbivore abundance, with an emphasis on gall-inducing insects. In: Price, P. W.; Slobodchikoff, C. N. & Gaud, W. S. *A new ecology: novel approaches to interactive systems*. John Wiley and Sons. pp.101-139.

FOLLIOT, R. 1964. Contribution à l'étude de la Biologie des Cynipides gallicoles (Hyménoptères, Cynipoidea). *Ann. Sci. Naturelles, Zool*., 12e series, t. VI: 407-564.

FOLLIOT, R.; ROS-FARRÉ, P.; BELLIDO, D. & PUJADE-VILLAR, J. 2003. Alternation of generations in *Andricus corruptrix* (Schlechtendal): comments and description of a new sexual form (Hym.: Cynipidae). *Contributions to Zoology* (in press).

GIBSON, G. A. P. 1985. Some pro- and mesothoracic structures important for phylogenetic analysis of Hymenoptera, with a review of terms used for the structures. *Canadian Entomologist*, 117: 1395-1443.

HARRIS, R. A. 1978. A glossary of surface sculpturing. *California Department of Food and Agriculture Laboratory Services. Entomology Occasional Papers*, 28: 1-31.

HARTIG in ROSENHAUER. 1856. Hymenoptera in *Die Thiere Andalusiens nach dem Resultate einer Reise*. pp. 368-375.

HESS, M. D.; ABRAHAMSON, W. G. & BROWN, J. M. 1996. Intraspecific competition in the goldenrod ball-gallmaker (*Eurosta solidaginis*): Larval mortality, adult fitness, ovipositional and host-plant response. *Am. Midl. Nat*., 136: 121-133.

HEWITT, G. M., 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, 58: 247-276.

KIEFFER, J. J. 1897-1901. *Monographie des Cynipides d'Europe et d'Algerie. Ibalynae et Cynipinae*. Paris. Lib. Scient. A. Hermann. 689 pp. 27 pl.

KIEFFER, J. J. 1901. Synopsis des Zoocecidies d'Europe. *Ann. Soc. Ent. fr*., 70: 233-579.

KINSEY, A. C. 1920. Phylogeny of cynipid genera and biological characteristics. *Bullet. Am. Mus. Nat. Hist*., 42, 357-402.

MAI, D. H. 1995. *Tertiäre Vegetationsgeschichte Europas. Methoden und Ergebnisse*. Gustav. Fischer Verlag. Jena

MARSDEN-JONES, E. M. 1953. A study of the life-cycle of *Adleria kollari* Hartig, the marble or Devonshire gall. *Trans. R. Ent. Soc. London*., 104: 195-221.

MELIKA, G. & CSÓKA, G. 1993. Comparing the oak galling cynipid fauna of Transcarpathia with that of Northern Hungary and the rest of the Ukraine. In: *The ecology and evolution of gall-forming insects*. Price, P. W., Mattson, W. J., & Baranchikov, Y. N. (Eds.). Proceedings of the international symposium; 1993 August 9-13; Krasnoyarsk, Siberia. Gen. Tech. Rep. NC-174. St. Paul, MN: USA. Department of Agriculture, Forest Service, North Central Research Station: 96-101.

MELIKA, G,, CSÓKA, G. & PUJADE-VILLAR, J. 2000. Check-list of oak gall wasps of Hungary, with some taxonomic notes (Hymenoptera: Cynipidae, Cynipinae, Cynipini). *Annls. hist.-nat. Mus. natn. hung.*, 92: 265-296.

NIEVES-ALDREY, J. L. , 1987. Estado actual del conocimiento de la subfamilia Cynipidae (Hymenoptera, Parasitica, Cynipidae) en la Península Ibérica. *Eos*, 63: 179-195.

NIEVES-ALDREY, J. L. 2001. *Hymenoptera, Cynipidae*. In: *Fauna Ibérica*, vol. 16. Ramos, M. A. *et al.* (Eds.). Museo Nacional de Ciencias Naturales. CSIC. Madrid. 636 pp.

PLANTARD, O.; RASPLUS, J.-Y. & HOCHBERG, M. E. 1996. Resource partitioning in the parasitoid assemblage of the oak galler *Neuroterus quercusbaccarum* L. (Hym.: Cynipidae). *Acta Oecologica*, 17(1): 1-15.

PUJADE-VILLAR, J. 1991. *Contribució al coneixement dels cinípids cecidògens dels arbres i arbusts de Catalunya, dels cinípids associats a aquests i dels seus paràsits*. Tesi doctoral. Universitat de Barcelona. 1128 pp.

PUJADE-VILLAR, J. 1992. *Andricus kollari* (Htg.) (Insecta: Hymenoptera: Cynipidae) 20 part: Consideracions sobre el seu cicle biològic. *La Sitja del Llop*, 3: 12.

PUJADE-VILLAR, J. 1997. Malformacions produïdes per cinípids als borrons de les fagàcies detectades a Andorra (Hym., Cynipidae). *Annals de l'Institut d'Estudis Andorrans, Centre de Barcelona*, 1997(1995): 13-39.

PUJADE-VILLAR, J. 2002. Comentario bibliográfico: una presentación excelente para un volumen con demasiados errores (Nieves-Aldrey, J. L., 2001 Hymenoptera Cynipidae, Fauna Ibérica). *Boln. Asoc. esp. Ent.* 26: 143-159.

PUJADE-VILLAR, J. & BELLIDO, D. 2000. Sobre las especies de cinípidos (Hymenoptera, Cynipidae) descritas por Hartig en la Sierra de Ronda. *Boln. Asoc. Esp. Ent.*, 24: 260-261.

PUJADE-VILLAR, J.; VILLEMANT, C. & ANDREI-RUIZ, M. C. 2000. Cynipidae associated with *Quercus* collected in Corsica with the description of a new *Plagiotrochus* species. *Zoosystema*, 22(4): 835-846.

ROBERTS, N. 1989. *The Holocene, an environmental history*. Basil Blackwell. 227 pp.

ROKAS, A.; ATKINSON, R. J.; WEBSTER, L.; CSÓKA, G. & STONE, G. N. 2003. Out of Anatolia: longitudinal gradients in genetic diversity support an eastern origin for a circum-Mediterranean oak gallwasp *Andricus quercustozae*. *Molecular Ecology*, 12: 2153-2174.

RONQUIST, F. & NORDLANDER, G. 1989. Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibaliidae). *Entomologica Scandinavica. Supplement*, 33: 1-60.

SCHÖNROGGE, K.; WALKER, P. & CRAWLEY, M. J. 1998. Invaders on the move: parasitism in the galls of four alien gallwasps in Britain (Hymenoptera: Cynipidae). *Proceedings of the Royal Society of London*, B, 256: 1643-1650.

SHORTHOUSE, J. D. 1988. Occurrence of two gall wasps of the genus *Diplolepis* (Hymenoptera: Cynipidae) on the domestic shrub rose, *Rosa rugosa* Thunb. Rosaceae. *Can. Ent.*, 120: 727-737.

SHORTHOUSE, J. D. 1994. Host shift of the leaf galler *Diplolepis polita* (Hymenoptera: Cynipidae) to the domestic shrub rose *Rosa rugosa*. *Can. Ent.*, 126: 1499-1503.

SHORTHOUSE, J. D. & BROOKS, S. E. 1998. Biology of the galler *Diplolepis rosaefolii* (Hymenoptera: Cynipidae), its associated component community, and host shift to the shrub rose Thèrese Bugnet. *Can. Ent.*, 130: 357-366.

SITCH, T. A.; GREWCOCK, D. A. & GILBERT, F. S. 1988. Factors affecting components of fitness in a gall-making wasp (*Cynips divisa* Hartig). *Oecologia*, 76: 371-375.

SITTE, P.; ZIEGLER, H.; EHRENDORFER, F. & BRESINSKY, A. 1994. *Strasburger, Tratado de Botánica*. 80 ed. Omega ed. Barcelona. 1070 pp.

STONE, G.; ATKINSON, R.; ROKAS, A.; CSÓKA, G. & NIEVES-ALDREY, J. L. 2001. Differential success in northwards range expansion between ecotypes of the marble gallwasp *Andricus kollari*: a tale of 2 lifecycles. *Molecular Ecology*, 10: 761-778.

TAVARES, J. da SILVA. 1902. As zoocecidias portuguezas. Addenda, com a descripçao de quinze especies cecidogenicas novas, *Brotéria*, 1: 1-100.

TAVARES, J. da SILVA. 1916. Especies e variedades novas de cinípides e Cecidomyias da Peninsula Iberica e descripçao de algunas ja conhecidas. *Brotéria Série Zoologica*, 14: 65- 136.

TAVARES, J. da SILVA. 1931. Os Cynipides da Peninsula Ibérica. *Brotéria. Ser. Zool.* 27: 5- 100.

TOUMI, L. & LUMARET, R. 1998. Allozyme variation in cork oak (*Quercus suber* L.): The role of phylogeography and genetic introgression by other Mediterranean oak species and human activities. *Theoret. and Appl. Genet.*, 97(4): 647-656.

WASHBURN, J. O. & CORNELL, H. V. 1981. Parasitoids, patches, and phenology: their possible role in the local extinction of a cynipid gall wasp population. *Ecology*, 62(6): 1597- 1602.

WEBB, T. & BARTLEIN, P. J. 1992. Global changes during the last 3 million years: climatic controls and biotic responses. *Annual Review of Ecology and Systematics*, 23: 141-173.

WIEBES-RIJKS, A. A. 1978. The sexual generation of the *Andricus kollari* -group in The Netherlands (Hymenoptera, Cynipidae). *Entomologische Berichten*, 38: 139-142.

WILLIS, K. J. 1992. The late Quaternary vegetational history of Northwest Greece. III. A comparative study of two contrasting sites. *New Phytologist*, 121: 139-155.

WILLIS, K. J. 1994. The vegetational history of the Balkans. *Quat. Sci. Rev.*, 13: 769-788.