



Oak associated inquilines  
(Hymenoptera, Cynipidae, Synergini)

Zsolt Péntzes, Chang-Ti Tang, Péter Bihari,  
Miklós Bozsó, Szabina Schwéger and George Melika

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## Introduction

Cynipidae lies within the superfamily Cynipoidea of the Hymenoptera, which includes approximately 3000 described species (Fergusson 1995, Ronquist 1999). With the exception of the Cynipidae and a group of gall-inhabiting inquiline genera in Figitidae, the cynipoids are all parasitoids, and probably cynipid gallwasps have evolved from parasitoid ancestors (Ronquist 1995, 1999). Cynipid gallwasps (Hymenoptera: Cynipidae) induce some of the world's most visually striking, and structurally complex plant galls. Approximately 1400 cynipid gallwasp species are currently recognized (Liljeblad and Ronquist 1998, Ronquist 1999, Ronquist and Liljeblad 2001, Nieves-Aldrey 2001, Melika 2006), although Nordlander (1984) has estimated that the actual number is between 3000 and 6000.

For historical reasons, all extant gallwasps belong to the subfamily Cynipinae and are divided into two main trophic groups: the gall inducers and the gall-associated inquilines, which together make up eight tribes (Csóka *et al.* 2005, Liljeblad *et al.* 2011). These are mainly characterized using biology and host plant data in combination with some morphological features. The Cynipini, Diplolepidini, Pediaspidini and Eschatocerini comprise the typical gall wasps found on oaks and roses as well as on some other woody plants of the eudicot subclass Rosidae (collectively called the woody rosid gallers). All gall inducers on herbaceous plants (+ some *Rubus*), from a wide variety of plant families, belong to the paraphyletic assemblage “Aylacini” (Melika 2006, Liljeblad *et al.* 2011). Recently, a unique South African tribe Qwaqwaiini was described, with only one known genus and species, *Qwaqwaia scolopiae* Liljeblad, Nieves-Aldrey and Melika which induces galls on *Scolopia mundii* (Salicaceae) (Liljeblad *et al.* 2011). The seventh tribe known from South America, the Paraulacini, originally were thought to be inquilines, like Synergini, however, judging from larval biology and by the fact that they are lethal to the gall inducing *Aditrochus* (Chalcidoidea: Pteromalidae: Ormocerinae) host species on *Nothofagus* (Nothofagaceae), it is entirely possible that they are parasitoids (Nieves-Aldrey *et al.* 2009).

Another lineage, distinct from the woody rosid gallers and other mentioned gall inducing tribes, gave rise to the tribe Synergini (*ca.* 185 species), whose members are all inquiline inhabitants of the galls of other cynipid gall wasps (Nylander 2004a, Liljeblad *et al.* 2008, Liljeblad *et al.* 2011). Although phytophagous, and able to induce the development of nutritive tissues within galls of other cynipids, they are apparently unable to induce their own galls *de novo*. The differences between gall-inducing cynipid wasps and cynipid inquilines are

thus not only morphological, but also represent an important and obvious biological division within the subfamily.

A number of review-like papers were published on the tribe Synergini in the last decade, however, all of them were fragmentary, either dealing with the morpho-taxonomy of the tribe, emphasized on a particular zoogeographical region/particular genus or only phylogenetic approach was given (Nieves-Aldrey 2001, Pujade-Villar *et al.* 2003, Csóka *et al.* 2005, Sadeghi *et al.* 2006, Péntzes *et al.* 2009, Ács *et al.* 2010, Melika *et al.* 2012). Since many new data were published on Synergini, especially with the description of new genera and species from the Eastern Palaearctic, Oriental and Neotropical Regions, which nobody yet generalized. In this paper we try to review our current knowledge of the Synergini tribe, focusing on the morphologically, systematically and phylogenetically most controversial Synergus-complex of genera, together with analysing the most recent unpublished phylogenetic result.

## **Main characteristics of the tribe Synergini**

*Inquilinism.* The term inquiline is derived from the Latin “inquilineus” meaning tenant or guest. Inquilinism is usually considered to represent a unilaterally beneficial relationship that benefits only the inquiline (Askew 1984). It is a form of cleptoparasitism (termed agastoparasitism by Ronquist (1994)). However, the real (obligate) inquilinism in cynipids is much more than a simple unilateral interaction (Askew 1984, Ronquist 1994, Csóka *et al.* 2005). As strictly defined, it is an obligatory relationship between two species in which the benefits are entirely unilateral but without detrimental effects on the partner. There are many examples of inquilinism in Hymenoptera, especially in the social hymenopteran groups of bees, wasps and ants (Askew 1984). In cynipid galls this definition applies to a taxonomically diverse group that includes inquiline gallwasps and their close cynipoid relatives, moths, beetles and gall midges. This paper focuses on the inquiline cynipids that feed obligately on plant tissues within developing galls and to some extent, stimulate the development of tissues characteristic to galls. The hymenopteran inquilines in cynipid galls are all cynipoids, and are either members of the cynipid tribe Synergini (Cynipidae), or figitids (Figitidae) in the subfamilies Parnipinae, Thrasorinae and Euceroptinae (Ronquist and Nieves-Aldrey 2001, Ross-Farré and Pujade-Villar 2007, Buffington and Liljeblad 2008).

*Gall-inducing ability in inquilines.* The inquiline cynipids have lost the ability to induce their own galls *de novo*. Nevertheless, they have retained the ability to modify the gall tissue directly surrounding them into the characteristic nutritive tissue also found in the larval chambers of the gall inducer, and all are wholly phytophagous. Some inquiline cynipids can substantially modify gall

structures outside the nutritive tissues, and the entire gall can be either enlarged (Shorthouse 1973, 1980) or stunted (Washburn and Cornell 1981; Wiebes-Rijks 1982) depending on the number of larvae in the gall. For example, when the unilocular galls of the rose cynipid gallwasp *Diplolepis nodulosa* (Beutenmüller) are attacked by the inquiline *Periclistus pirata* (Osten Sacken), the result is a gall three times the size of one inhabited only by the gall inducer, and contains 17 inquiline larval chambers (Brooks and Shorthouse 1998). The most dramatic modification of host gall structure by an inquiline cynipid in oak galls is that caused by members of the genus *Synophrus*. *S. politus* Hartig attacks, at a very early stage, tiny sexual generation cynipid galls induced by species in the “*Andricus burgundus*” complex (Pujade-Villar *et al.* 2003). Whilst most other cynipid inquilines induce differentiation of nutritive tissues in a developing host gall exclusively, the *Synophrus* larva appears to control differentiation of the whole gall and only lacks the ability to initiate gall induction. Feeding activity of the larvae on the chamber walls is thought to induce the growth and differentiation of the gall tissues, as is the case for cynipid gall inducers. The gall of *S. politus* is unilocular, and the larva moves freely within a large cavity. However, the appearance of “*Synophrus* galls” is unstructured comparing to the variety of galls of true inducers (Cynipini), so the nature of interaction with the host plant and their share in gall development remain to be explored. More striking even is the recently described new inquiline species, *Synergus itoensis* Abe, Ide and Wachi from Japan, for which rearing experiments demonstrated gall induction in the seed coat of the acorn of *Quercus glauca* Thunb. (Abe *et al.* 2011). All of these changes, caused by inquilines, have the potential to significantly modify parasitoid attack rates and so to influence mortality rates in inquilines and gall inducers. The inquiline influences may be more generally important than is currently known (Sanver and Hawkins 2000).

*Effects on the host gall larvae: lethal and non lethal inquilines.* Some cynipid inquilines kill the host larva early in the development of the gall. However, this is not a trophic relationship since they do not feed on the host larva. It appears that where inquiline eggs are placed in close proximity to the gall-inducer's larval chambers, the more rapid development of the inquiline larvae and their chambers crushes the gall inducer (Weld 1952, Evans 1965, Shorthouse 1973, 1980, Wiebes-Rijks 1979). An inquiline can be lethal in one type of gall, but develop in the peripheral tissues of another host gall with no apparent harm to the original gall-inducer (Mayr 1872, Nieves-Aldrey 2001). A subset of inquiline cynipids (termed lethal inquilines, Duffet 1968) inflicts substantial mortality on gall inducers. In oak cynipid galls, inquilines can be divided into those whose larval chambers occupy the host larval chamber, and those whose chambers develop in outer gall tissues. Closely related inquilines may have quite different impacts on their host: For example, in the asexual generation galls of the oak cynipid gall wasp *Andricus kollari* (Hartig), *Synergus reinhardi* Mayr is a lethal inquiline in

the larval chamber, while *Synergus umbraculus* (Olivier) develops in the outer wall of the gall and has no obvious negative effect on the gall inducer (Schönrogge *et al.* 1996, 2000). When attacked by non-lethal inquilines, both inquilines and the gall inducer may emerge from a single gall. The total numbers emerging are the highest when non-lethal inquilines (such as *S. umbraculus*, *S. facialis* Hartig and *S. pallicornis* Hartig) infest the outer gall parenchyma of large host galls, as in case of *Andricus quercuscalicis* (Burgsdorf) (Schönrogge *et al.* 1996).

*The biology of inquiline immature stages.* The morphology of the immature stages of cynipid inquilines are already discussed in some papers (Vårdal *et al.* 2003, Nieves-Aldrey *et al.* 2005) as well as their biology. The most detailed studies were made on *Periclistus pirata* (Osten Sacken) inquilines in galls induced by the rose gallwasps *Diplolepis polita* (Ashmead) and *D. nodulosa* (see for example, Shorthouse 1973, Brooks and Shorthouse 1998).

*Inquiline life cycles and phenology.* Most species have similar life cycles, with a single generation per year synchronised with their hosts. Adults usually emerge from the galls after the gall inducers and lay eggs in freshly initiated galls. Part of the species, especially in the *Synergus* genus, produce two generations per year and some of them show generational dimorphism (for example, *Synergus facialis*) (Wiebes-Rijks 1979, Melika 2006).

## **Taxonomy, diversity and distribution of inquiline cynipids: Tribe Synergini Ashmead, 1896**

The adult cynipid inquilines are insects of small to moderate size, from 0.8 to 7 mm in body length, and share the following morphological characters: genae not or weakly expanded behind eyes; lower face usually with radiating striae from clypeus reaching antennal rims; clypeus indistinct and ventral clypeal margin straight; subocular sulcus absent; distance between occipital and oral foramina longer than height of occipital foramen; long postgenal sulci and postgenal ridges united well before reaching hypostomata; maxillary palp 5-segmented; labial palp with three segments. Antenna of female with 12–14 segments; antenna of male with 14–15 segments, with first flagellomere usually more or less expanded apically. Mesosoma sculptured. Pronotum relatively long, measuring medially 1/5 to 1/3 of the shortest distance across lateral margin; pronotal pits (admedian depressions) usually conspicuous and separated medially, sometimes associated with a weak pronotal plate; lateral pronotal carinae present or not; lateral longitudinal carinae of propodeum subparallel. Fully winged except for some males of *Synergus thaumacerus*; tarsal claws with an acute basal lobe or tooth. Metasoma with the second tergum reduced or ring shaped and dorsally with longitudinal ridges (sulcate); third and fourth abdominal terga free or usually fused and covering almost all the metasoma; prominent part of the ventral spine of hypopygium short.

The taxonomic position and classification of the cynipid inquilines has long been controversial, but has recently been clarified somewhat (Pujade-Villar *et al.* 2003, Péntzes *et al.* 2009), nevertheless some genera are still problematic, especially on the species level (Ács *et al.* 2010). Hartig (1840) was the first to recognise the biological differences between the inquiline and gall forming Cynipidae. He described the genera *Ceroptres*, *Synergus* and *Synophrus* as inquilines from oak galls, although he regarded *Synophrus* as a gall inducing genus (Hartig 1840, 1843). At different times the cynipid inquilines have either been placed in a separate subfamily within the Cynipidae (Hartig 1840, Ashmead 1896a, 1903), included in the herb gall wasp tribe Aylacini (Roskam 1992), or lumped with the gall inducers into a large group without subdivisions (Weld 1952, Eady and Quinlan 1963). However, more recently they have been classified as belonging to the tribe Synergini within the Cynipidae (Burks 1979, Ronquist 1999, Melika 2006).

The entire world fauna of the tribe Synergini includes 186 species of inquilines in nine genera (Table 1): six genera, *Agastoroxenia* Nieves-Aldrey & Medianero, 2010, *Ceroptres* Hartig, 1840, *Saphonecrus* Dalla Torre & Kieffer, 1910, *Synergus* Hartig, 1840, *Synophrus* Hartig, 1843 and *Ufo* Melika & Pujade-Villar, 2005, form the *Synergus*-complex of genera and all are inquilines in cynipid galls on oak and oak-relative genera within Fagaceae (Csóka *et al.* 2005, Melika *et al.* 2005, van Noort *et al.* 2007, Ács *et al.* 2010, Nieves-Aldrey and Medianero 2010). Inquiline cynipids associate with cynipid galls on roses (Diplolepidini) are represented with only one genus *Periclistus* Förster, 1869. *Synophromorpha* Ashmead, 1903 are inquilines in *Diastrophus* galls on *Rubus* (Rosaceae) (Ritchie 1984). The mentioned 8 genera are distributed mainly in the temperate zone of the northern hemisphere, in the Holarctic region, however, *Agastoroxenia* is known only from the Neotropics, as well as 14 *Synergus* species known from Panama and Guatemala (Nieves-Aldrey and Medianero 2011 and Table 1). Few oak gall associated inquiline species are known also from the Oriental region: two *Saphonecrus* species from the Philippines (Weld 1926), some newly described *Saphonecrus* species from the Oriental Region of China (Wang *et al.* 2010, Liu *et al.* 2012) and 1 species of *Ufo* from Taiwan (Melika *et al.* 2012).

The genus *Rhoophilus* Mayr, 1881 raises an interesting biogeographic problem. This genus is known only from a single species, *R. loewi* Mayr, 1881 and is the only cynipid genus restricted to the Ethiopian region in South Africa (Mayr 1881, van Noort *et al.* 2007). No inquiline cynipids are known from Eschatocerine cynipid galls, very few attack aylacine cynipid galls - the exceptions are *Synophromorpha* species that develop in *Diastrophus* cynipid galls on bramble, *Rubus* (Ritchie and Shorthouse 1987b). A marked feature of cynipid inquilines is that they are generally more specific to a particular plant taxon than they are to a given host gall inducer.

Table 1. The world distribution and species richness of Synergini genera (WP, Western Palaearctic, EP, Eastern Palaearctic, OR, Oriental Region, NA, Nearctic, NT, Neotropical Region, ET, Ethiopian Region).

Genera	Hosts	WP	EP	OR	NA	NT	ET	<b>World</b>
<i>Agastoroxenia</i> Nieves-Aldrey et Medianero, 2010	Oak cynipid galls	–	–	–	–	1	–	<b>1</b>
<i>Ceroptres</i> Hartig, 1840	Oak cynipid galls	2	4	–	17	–	–	<b>23</b>
<i>Synergus</i> Hartig, 1840	Oak cynipid galls	30	10	–	55	14	–	<b>109</b>
<i>Saphonecrus</i> Dalla Torre & Kieffer, 1910	Oak cynipid galls	6	9	2	4	–	–	<b>21</b>
<i>Synophrus</i> Hartig, 1843	Oak cynipids	7	–	–	–	–	–	<b>7</b>
<i>Ufo</i> Melika & Pujade, 2005	Oak cynipid galls	–	3	1	–	–	–	<b>4</b>
<i>Periclistus</i> Förster, 1869	<i>Rosa</i> cynipid galls	3	4	–	7	–	–	<b>14</b>
<i>Synophromorpha</i> Ashmead, 1903	<i>Rubus</i> galls	–	2	–	4	–	–	<b>6</b>
<i>Rhoophilus</i> Mayr, 1881	<i>Rhus</i> galls	–	–	–	–	–	1	<b>1</b>
<b>Total:</b>		<b>48</b>	<b>32</b>	<b>3</b>	<b>87</b>	<b>15</b>	<b>1</b>	<b>186</b>

The number of known Synergini species (Table 1) is unevenly distributed between the zoogeographical regions. Pujade-Villar *et al.* (2003) revised the Synergini of the Western Palaearctic and synonymised 29 doubtful species, Sadeghi *et al.* (2006) described 5 new species from Iran and, thus bringing the number of recognised species in the Western Palaearctic to 48 species. No doubt, the most studied region is the Western Palaearctic and the number of described species probably will not change essentially with further research. The number of Eastern Palaearctic species increased essentially during the last decade and the growing tendency will stay because of the activity of some cynipid research groups in China and Taiwan. The same growing tendency characterizes the Neotropics, where a considerable number of new species was described during the last years (Nieves-Aldrey and Medianero 2010, 2011). The high number of inquiline species described from the USA and Canada is inadequate to the number of species known from Mexico. Research in Mexico will definitely recon the hidden diversity of Synergini in the large and very peculiar faunistic and floristic zones of the country.

Despite the shared characters given above, the Synergini represents a polyphyletic assemblage of inquiline lineages, which we shall discuss in details later. Below we give a brief taxonomic overview of all known Synergini genera, with short morphology, taxonomic assignment and diversity. The non-oak host related genera (*Periclistus*, *Synophromorpha* and *Rhoophilus*) are briefly discussed below while the oak and near oak-related host genera, *Ceroptres* and the Synergus complex of genera (*Agastoroxenia*, *Saphonecrus*, *Synergus*, *Synophrus* and *Ufo*), are given in details.

### ***Periclistus* Förster, 1869**

Type species: *Aylax caninae* Hartig, 1840.

*Periclistus* is very similar to *Ceroptres* in the shape of the first metasomal tergite but females have the 2<sup>nd</sup> metasomal tergite completely fused with the 3<sup>rd</sup> (a suture present between them in males). Head and mesosoma black, metasoma chestnut brown, with darker posterior tergites. Antenna and legs yellow to partially chestnut brown; coxae dark brown to black. Head delicately coriaceous to alutaceous, nearly as high as broad in front view; gena not broadened behind eye; malar space very short, much shorter than height of eye; malar space and lower face with strong striae, radiating from clypeus and reaching eye and antennal sockets. Clypeus small, quadrangular, slightly higher than broad, with distinct anterior tentorial pits, clypeo-pleurostomal line and epistomal sulcus; ventrally rounded, not projecting over mandibles. Frons, vertex, occiput, postocciput and postgena delicately coriaceous to alutaceous. POL slightly longer than OOL; transfacial distance slightly shorter than height of eye. Antenna filiform, 12–13-segmented in female and 14-segmented in male. Scutum uniformly delicately coriaceous; notauli complete, although sometimes weakly impressed; median mesoscutal line usually extending at least to half of scutum length. Scutellum rugose, with more delicate sculpture towards center of scutellar disk and in between scutellar foveae. Scutellar foveae transversely ovate, only slightly broader than high, well-delimited around, separated by central carina. Mesopleuron transversely striate. Lateral propodeal carinae subparallel; central propodeal area coriaceous, without setae; lateral propodeal area delicately uniformly coriaceous, with relatively dense white setae. Forewing margin with long cilia; radial cell closed, at least 3.0 times as long as broad, areolet distinct, Rs+M nearly reaching basalis. Metasomal tergites 2 and 3 fused in female, free in male, punctate in dorso-posterior part, sometimes punctures indistinct; prominent part of ventral spine of hypopygium very short (Fig. 1).

*Periclistus* has an Holarctic distribution with 14 known species (Table 2), which from seven species are known from America north of Mexico (Burks 1979); three species are known from the Western Palaearctic, *P. brandtii*, *P. caninae* and *P. idoneus* known from Israel only (Belizin 1973). Four species of *Periclistus* were described from the Eastern Palaearctic: *P. mongolicus* from Mongolia (Belizin 1973), *P. capillatus* from Primorskij Kraj of Russia (Belizin 1968), and two species, *P. natalis* and *P. quinlani* from Japan, from *Diplolepis japonica* (Walker) galls (Abe *et al.* 2007). *P. capillatus* and *P. natalis* were reared by one of the co-authors (GM) also from galls of *Liebelia fukudae* (Shinji) in the Far East of Russia and Hokkaido, Japan. Except *L. fukudae*, the genus *Liebelia*

Kieffer which associates with wild roses, is represented by other 7 species described from Kyrgyzstan, Kazakhstan, Uzbekistan and Siberia and no doubts, they support a number of undescribed *Periclistus* species (Belizin 1957, Vyrzhikovskaja 1963).



Figure 1. *Periclistus brandtii*: a–h, female: a, head, anterior view, b, head, dorsal view, c, mesosoma, anterodorsal view, d, mesosoma and propleura, anterior view, e, mesosoma, dorsal view, f, mesosoma, lateral view, g, forewing, part with radial cell, h, metasoma, lateral view. i, metasoma, lateral view, male.



Table 2. Known species of *Periclistus*: distribution and host associations.

<b>Species</b>	<b>Distribution</b>	<b>Host plants/galls</b>
<i>P. arefactus</i> McCracken & Egbert, 1922	NA: USA, California	<i>Diplolepis</i> sp. on wild roses
<i>P. brandtii</i> (Ratzeburg, 1831)	WP: entire	<i>Diplolepis</i> sp. on wild roses
<i>P. californicus</i> Ashmead, 1896	NA: USA, California	<i>Diplolepis</i> sp. on wild roses
<i>P. caninae</i> (Hartig, 1840)	WP: entire	<i>Diplolepis</i> sp. on wild roses
<i>P. capillatus</i> Belizin, 1968	EP: Russia, Primorskij Kraj	<i>Diplolepis</i> sp. and <i>Liebelia</i> sp. on wild roses
<i>P. idoneus</i> Belizin, 1973	WP: Israel	Unknown
<i>P. mongolicus</i> Belizin, 1973	EP: Mongolia	Unknown
<i>P. natalis</i> Taketani & Jasumatzu, 1973	EP: Japan	<i>Diplolepis</i> sp. and <i>Liebelia</i> sp. on wild roses
<i>P. obliquus</i> Provancher, 1888	NA: USA, California	<i>Diplolepis</i> sp. on wild roses
<i>P. piceus</i> Fullaway, 1911	NA: USA, California	<i>Diplolepis</i> sp. on wild roses
<i>P. pirata</i> (Osten Sacken, 1863)	NA: Eastern USA and Canada	<i>Diplolepis</i> sp. on wild roses
<i>P. quinlani</i> Taketani & Jasumatzu, 1973	EP: Japan	<i>Diplolepis</i> sp. on wild roses
<i>P. semipiceus</i> (Harris, 1841)	NA: USA, Massachusetts	<i>Diplolepis</i> sp. on wild roses
<i>P. smilacis</i> Ashmead, 1896	NA: USA, Florida	<i>Diastrophus smilacis</i> on <i>Smilax</i>
<b>Total: 14 species</b>		

The biology and hosts of *Periclistus idoneus* described from Israel are unknown yet (Belizin 1973). It is closely related to *P. brandtii* and must be revised in order to confirm its validity (Pujade-Villar *et al.* 2003). Another species, *P. spinosissima* Dettmer, reared from *Diplolepis spinosissima* (Giraud) and known from the Netherlands (Dettmer 1924) and Great Britain (Eady and Quinlan 1963) is closely related to *P. caninae* and must be revised in order to confirm its validity (Pujade-Villar *et al.* 2003).

*Periclistus* species are associated with *Diplolepis* and *Liebelia* rose galls, except one nearctic species, *P. smilacis* known from Florida and reared from galls of *Diastrophus smilacis* (Ashmead 1896a). This host association was doubted for a long time, however, one of the co-authors (GM, unpublished data) also reared *P. smilacis* adults from galls of *D. smilacis* on *Smilax* sp. (a monocot vine). All known gall wasps are associated with eudicots that is why this host shift is very unusual (Ronquist and Liljeblad 2001). The biology of *Periclistus* species has been studied in details in some holarctic species (e.g. Brooks and Shorthouse

1998, Shorthouse 1973, 1980). Larvae of some species can strongly modify the gall structure of the host (Shorthouse 1973, 1980). Two common Western Palaearctic species: *P. brandtii* usually attacks multilocular galls of *Diplolepis mayri* (Schlechtendal) and *D. rosae* (L.), while *P. caninae* usually attacks monolocular galls of *D. nervosa* (Curtis) and *D. eglanteriae* (Hartig). All *Periclistus* species are monovoltine and known from the sexual generations (Melika 2006).

### ***Synophromorpha* Ashmead, 1903**

Type species: *Synophrus sylvestris* Osten Sacken, 1861 (desig. In Ritchie and Shorthouse 1987b).

Originally *Synophromorpha salicis* Ashmead, 1903 was designated as the type-species. Unfortunately the type-species of this genus is from unknown locality and its host was supposed to be a dipterous gall-inducer on *Salix*. The type species has not been located and probably was lost (Weld 1952, Burks 1979). Details on the taxonomy, systematics, morphology, biology, host associations and phylogeny of *Synophromorpha* are given in Ritchie and Shorthouse (1987b). The genus is most similar to *Periclistus* and differs as follows: the mesoscutum is smooth to granulate, with strong setigerous punctures anteriorly; notauli are very strong, complete, in a form of distinct deep grooves; the ventral margin of the subalar triangle smooth, without rows of setigerous punctures; the maxillary palp with five segments; T1 smooth and crescent shaped, T2+3 fused in females but separate in males; the radial cell of the forewing is opened (Ritchie and Shorthouse 1987b).

Only 6 species of *Synophromorpha* are known: 4 from the Nearctic and 2 from the Eastern Palaearctic (Table 3).

Table 3. Known species of *Synophromorpha*: distribution and host associations.

<b>Species</b>	<b>Distribution</b>	<b>Host plants/galls</b>
<i>S. kaulbarsi</i> Ritchie & Shorthouse, 1987	NA: Mexico, Puebla, Naupan	Unknown
<i>S. rubi</i> Weld, 1952	NA: USA, Illinois	<i>Diastrophus</i> sp. on <i>Rubus</i>
<i>S. sylvestris</i> (Osten Sacken, 1861)	NA: USA, Eastern Coast	<i>Diastrophus</i> sp. on <i>Rubus</i>
<i>S. taketanii</i> Abe, 1998		Stem gall on <i>Rubus</i>
<i>S. terricola</i> Weld, 1952	NA: USA, DC and Virginia	<i>Diastrophus</i> sp. on <i>Rubus</i>
<i>S. tobiasi</i> Belizin, 1973	EP: Tajikistan, Kyrgyzstan	Unknown
<b>Total: 6 species</b>		

*Synophromorpha kaulbarsi* described from Mexico is the most plesiomorphic species in the genus and host associations are still unknown, probably some gall-inducers on *Rubus* (Ritchie and Shorthouse 1987b). *Synophromorpha tobiasi* is

known from Tajikistan and Kyrgyzstan (Belizin 1973). The taxonomic status of this species is uncertain and the type must be revised (Abe *et al.* 2007). The second Eastern Palearctic species, *S. taketanii*, was reared from stem swelling-like galls on *Rubus palmatus* in Japan, however, whether it is a *Diastrophus* gall or not must be clarified (Abe 1998, Abe *et al.* 2007).

### ***Rhoophilus* Mayr, 1881**

Type species: *Rhoophilus loewi* Mayr, 1881

*Rhoophilus* is morphologically related to the holarctic inquiline genera *Synergus*, *Saphonecrus*, and *Synophrus*, all of which typically attack oak cynipid galls. A sister group relationship between *Rhoophilus* and the oak inquiline genera *Synergus* + *Synophrus* + *Saphonecrus* was hypothesized by Ronquist (1994) and Liljeblad and Ronquist (1998). Shared diagnostic characters include the following: the ventral margin of the clypeau is straight not projecting over mandibles; radiating striae on the lower face reaching or almost reaching the compound eye; the distance between occipital and oral foramina is longer than the height of the occipital foramen; the position of the anterior end of the metapleural sulcus is high; the mesoscutum with strong transverse ridges, the mesopleuron also with longitudinal ridges; tarsal claws with a blunt small basal lobe.

The biology of *Rhoophilus loewi* has been controversial. Despite the fact that the species had always been classified with the inquiline cynipids, its host was unknown and the species was sometimes considered as the true gall inducer wasp on *Rhus* species (Anacardiaceae) (Dalla Torre and Kieffer 1910, Ronquist 1999). Recently it was demonstrated that *R. loewi* is an inquiline in galls induced by a cecidosid moth genus *Scyrotis* on *Rhus* species (Anacardiaceae) and thus, represents one of the few known cases where the host for a cynipid wasp is not itself a cynipid. *Rhoophilus* is a lethal inquiline; its larval cells expand into the hollow interior of the host gall resulting in death of the gall inducer (van Noort *et al.* 2007).

*Rhoophilus loewi* and the recently described south african cynipid gall-inducer *Qwaqwaia scolopiae* Liljeblad, Nieves-Aldrey & Melika on *Scolopia mundii* (Salicaceae) represent the only cynipid taxa with an Afrotropical distribution (Liljeblad *et al.* 2011). Ronquist and Liljeblad (2001) hypothesized that the gall wasps (Cynipidae) arose in Europe, around the Black Sea, and that the genera *Eschatocerus* (gall inducers on *Acacia* and *Prosopis*) and *Rhoophilus* apparently spread later to South America and South Africa, respectively. However, recent results may contradict this hypothesis. *Eschatocerus* and *Rhoophilus* may represent older primitive lineages of cynipids and as such the biogeographical history of the basal Cynipidae is still not clear (Nylander 2004a). The presence of *Rhoophilus*, *Qwaqwaia* and *Phanacis nesororum* Melika & Prinsloo in southern Africa, far from other centres of cynipid diversity, suggests that other african groups may await discovery (Melika and Prinsloo 2007, Liljeblad *et al.* 2011).

## ***Ceroptres* Hartig, 1840**

Type species: *Ceroptres clavicornis* Hartig, 1840.

Body predominantly black, rarely chestnut brown or even orange; antenna and legs light brown to yellow chestnut brown, except darker to black scape and coxae. Head alutaceous to delicately coriaceous, broader than high in front view, with sparse white short setae. Gena not broadened behind eye; malar space much shorter than height of eye, with striae radiating from clypeus and reaching eye. Transfacial distance shorter than height of eye; diameter of antennal torulus 3.0 times as large as distance between them and slightly longer than distance between torulus and eye margin. Inner margins of eyes slightly converging ventrally. Clypeus small, quadrangular, anterior tentorial pits, clypeo-pleurostomal line and epistomal sulcus distinct, ventral margin rounded, not projecting over mandibles. Lower face with striae radiating from clypeus and reaching inner margin of eye and antennal sockets, with two vertical more or less distinct raised carina running from antennal sockets and reaching or not clypeus. Frons, vertex and occiput uniformly alutaceous. Distance between occipital and oral foramina larger than height of occipital foramen; gular sulci united well above hypostoma. Antenna of female slightly clavate, 12-13-segmented, in male – 14-15-segmented; F2 slightly shorter or equal F1. Pronotum dorso-medially 1/3-1/2 times shorter than measuring along lateral outer margin; submedian pronotal pits narrow, transverse, separated by a median carina. Scutum delicately coriaceous to alutaceous; notauli complete, well-impressed along entire length or indistinct only in anterior 1/3; median mesoscutal line short, extending to 1/3 of scutum length or in a form of short triangle. Scutellum coriaceous to rugose, rounded, scutellar foveae transverse, more or less well-delimited posteriorly, separated by a distinct central carina. Mesopleuron smooth, shining, with some very delicate transverse striae, especially in antero-dorsal part; metapleural sulcus reaching mesopleuron in the upper 1/3 of its height. Lateral propodeal carina subparallel. Forewing with short cilia on margin, radial cell closed along wing margin. Tarsal claws with basal lobe. Metasoma nearly as high as long in lateral view; metasomal tergite 2 small, with dense setae antero-laterally and free, not fused with metasomal tergite 3, which occupying 2/3 or more of metasoma length. Prominent part of ventral spine of hypopygium very short (Fig. 2).

*Ceroptres*, at least the palaearctic species, has two main diagnostic morphological characters (autapomorphies): two raised vertical carinae on the lower face and the metasomal tergite 2 is free (not fused with metasomal tergite 3) and small (ratio of median length of metasomal tergite 2 to median length of tergite 3 <1.0). *Ceroptres* is also the only Synergini in cynipid galls on oaks with a smooth and shining metasomal tergite 1, reduced to a dorsal crescent-shaped scale, without sulci. While the European species of *Ceroptres* are distinct from other inquiline genera and particularly from *Synergus*, the situation for the nearctic species is less clear. Weld (unpublished data) found specimens that are intermediate between *Ceroptres* and *Synergus*. For example, the vertical carinae extending from the ventral margin of the antennal sockets (which are well-developed in European species) are incomplete or absent in the nearctic *Ceroptres* specimens. Ritchie (1984) believed similarities between *Synergus* and *Ceroptres* to support a close relationship between the two genera. This opinion has been supported by Liljeblad and Ronquist (1998), who stated that the North American

species of *Ceroptres* resemble other inquiline genera more than they do European species in the same nominal genus. However, close relationships between *Ceroptres* and *Synergus* are not supported by recent sequence-based molecular phylogenetic analyses, which find *Ceroptres* to represent a separate case for evolution of inquilinism of oak cynipid galls. Molecular phylogenies suggest that it is derived from a different gall-inducing ancestor which about we shall talk in details later (Nylander 2004a, Ács *et al.* 2010).

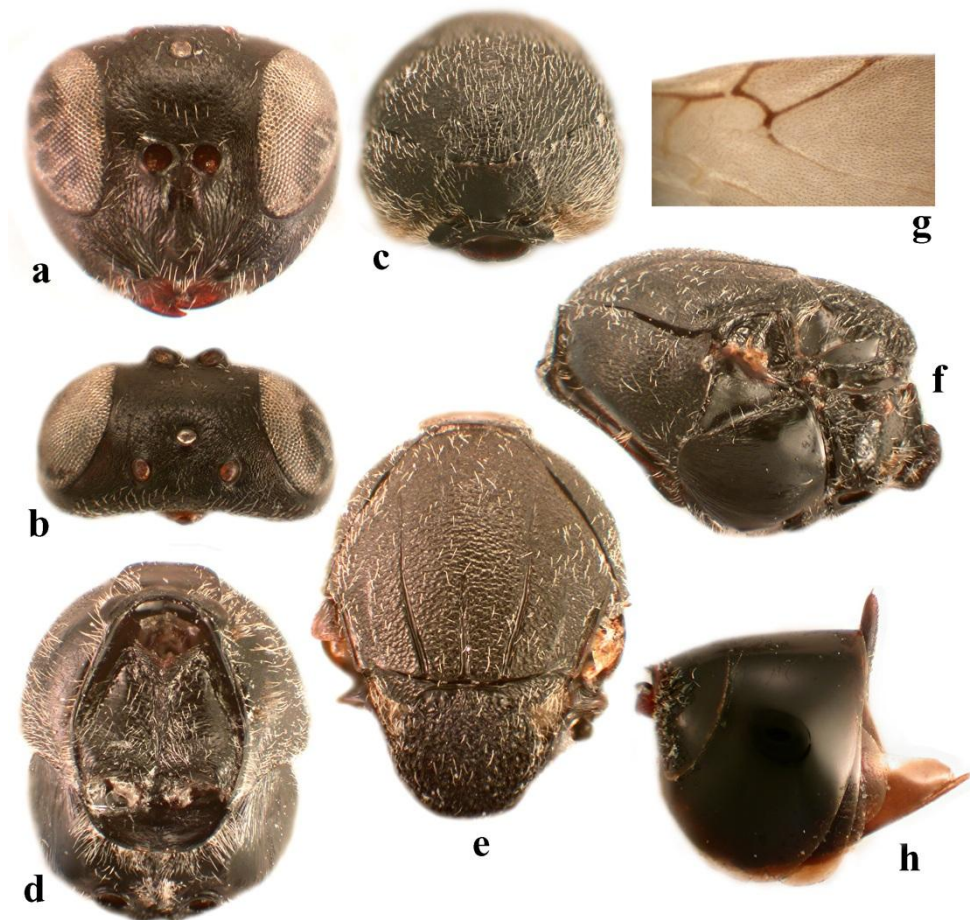


Figure 2. *Ceroptres cerri*, female: a, head, anterior view, b, head, dorsal view, c, mesosoma, anterodorsal view, d, mesosoma and propleura, anterior view, e, mesosoma, dorsal view, f, mesosoma, lateral view, g, forewing, part with radial cell, h, metasoma, lateral view.

*Ceroptres* is distributed throughout the Holarctic Region and 23 valid species are known (Table 4): six species from the Palearctic and 17 from the Nearctic (Ritchie 1984, Burks 1979, Melika and Buss 2002, Melika 2006, Abe *et al.* 2007, Wang *et al.* 2012).

Table 4. Known species of *Ceroptres*: distribution and host associations.

Species	Distribution	Host plants
<i>C. catesbaei</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. Lobatae
<i>C. cerri</i> Mayr, 1872	WP: entire	<i>Quercus</i> sect. Cerris
<i>C. clavicornis</i> Hartig, 1840	WP: entire	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. confertus</i> (McCracken & Egbert, 1922)	NA: USA, California	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. cornigera</i> Melika & Buss, 2002	NA: Eastern USA	<i>Quercus</i> sect. Lobatae
<i>C. distinctus</i> Wang, Liu & Chen, 2012	EP: China (Zhejiang)	Unknown
<i>C. frondosae</i> Ashmead, 1896	NA, USA, Missouri	Unknown
<i>C. inermis</i> (Walsh, 1864)	NA: USA, Illinois	Gall-midges on <i>Lobatae</i> oaks
<i>C. kovalevi</i> Belizin, 1973	EP: Russia, Primorskij Kraj	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. lanigerae</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. masudai</i> Abe, 1997	EP: Japan, Korea, Russia, China	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. minutissimi</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. montensis</i> Weld, 1957	NA: USA, California	<i>Quercus</i> sect. Protobalanus
<i>C. niger</i> Fullaway, 1911	NA: USA, California	Unknown
<i>C. petiolicola</i> (Osten Sacken, 1861)	NA: Eastern USA	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. politus</i> Ashmead, 1896	NA, USA, Virginia	Unknown
<i>C. quercusarbos</i> (Fitch, 1859)	NA: USA, New York	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. quercusficus</i> (Fitch, 1859)	NA: USA, New York	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. quercusobtusilobae</i> (Karsch, 1880)	NA: USA, Texas	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. quercuspisum</i> (Fitch, 1859)	NA: USA, New York	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. quercustuber</i> (Fitch, 1859)	NA: USA, New York	<i>Quercus</i> sect. <i>Quercus</i>
<i>C. rufiventris</i> Ashmead, 1896	NA, USA: Missouri	<i>Quercus</i> sect. Lobatae
<i>C. setosus</i> Wang, Liu & Chen, 2012	EP: China (Zhejiang)	Unknown
<b>Total: 23 species</b>		

Four Eastern Palaearctic species, *C. distinctus*, *C. kovalevi*, *C. masudai* and *C. setosus* are known. *Ceroptres kovalevi* and *C. masudai* associate with galls on white oaks and are known from the Far East of Russia and Japan, Korea, Russia, China, respectively (Belizin 1973, Abe 1997, Abe *et al.* 2007, Wang *et al.* 2012). Host gall and host plant associations of two species from China, *C. distinctus* and *C. setosus*, are unknown (Wang *et al.* 2012).

The nearctic species have never been revised and it is very difficult to identify any of them, 16 species were listed in Burks (1979), and the only one species, *C. cornigera*, known to associate with stem galls on red oaks, was described later (Melika and Buss 2002).

## **Synergus complex of genera**

Inquilines of the tribe Synergini attack the galls in the gallwasp tribes Cynipini (oak gallwasps, hosts to the inquiline genera *Agastoroxenia*, *Ceroptres*, *Saphonecrus*, *Synergus*, *Synophrus* and *Ufo*), Diplolepidini (rose gallwasps, hosts to the inquiline genus *Periclistus*), Aylacini (herb gallwasps, hosts to the inquiline genus *Synophromorpha*) and galls induced by Cecidosid moths on *Rhus* (hosts to the inquiline genus *Rhoophilus*) (Ronquist 1994, 1999, Csóka *et al.* 2005, van Noort *et al.* 2007). The morphological taxonomy of the inquilines which attack hosts in the gallwasp tribes Cynipini has been studied in details (Mayr 1872; Wiebes-Rijks, 1979; Nieves-Aldrey and Pujade-Villar 1985, 1986; Pujade-Villar and Nieves-Aldrey 1990, 1993; Liljebald and Ronquist 1998; Liljebald *et al.* 2008; Pujade-Villar *et al.* 2003, Melika 2006) and showed that five genera, *Agastoroxenia*, *Saphonecrus*, *Synergus*, *Synophrus* and *Ufo* morphologically differ from *Ceroptres* and form a distinct monophyletic lineage, which we call the Synergus complex of genera.

### ***Agastoroxenia* Nieves-Aldrey & Medianero, 2010**

Type species: *Agastoroxenia panamensis* Nieves-Aldrey & Medianero, 2010.

The genus is readily differentiated from other genera of Synergini by 13-segmented antenna in both females and males; pedicel relatively long, 2.5 times longer than broad and longer than scape and F2; F1 of male antenna strongly curved dorsally, excavated medially, and expanded apically and basally. Metatarsal claws with small basal tooth, less than one third as long as the apical tooth. Gena expanded behind compound eye; frontal carinae present, branched near ocellar plate and vertex; irradiating lower face striae strong, broad and blunt; ventral margin of clypeus slightly projected over mandibles; lower face with irregular longitudinal rugae medially; distance between occipital foramen and oral foramen shorter than height of occipital foramen; postgenal sulci meet at middle part of postgenal bridge. Lateral pronotal carina indistinct; notauli complete but faint in anterior one third of mesoscutum; mesoscutum with transverse interrupted and spaced rugae; mesopleuron longitudinally striate with coriaceous sculpture between striae;

scutellar foveae large, inner margins widely diverge and opened posteriorly; lateral propodeal carina broad, subparallel; radial cell obsoletely closed on wing margin by depigmented R1, T2–3 covering 95% of metasoma; ventral projection of hypopygium as long as high.

Morphologically, *Agastoroxenia* is related to *Saphonecrus* and *Synophrus* by the 13-segmented antenna in females, however, in males the antenna is also 13-segmented which is a unique autapomorphic feature among all the known genera of Synergini. With slightly expanded genae, weakly sulcated dorsal part of 1st metasomal tergite and the general sculpture of the mesoscutum and mesopleuron, this genus resembles *Synophrus*, but it has strong frontal carinae, a character state that is shared by the majority of the *Synergus* species.

This genus, with one known species, *Agastoroxenia panamensis* Nieves-Aldrey & Medianero, is distributed in Panama, an inquiline reared from an unidentified *Andricus* stem gall on *Q. lancifolia* (*Quercus* section, Lobatae) (Nieves-Aldrey and Medianero 2010).

### ***Saphonecrus* Dalla Torre et Kieffer, 1910**

Type species: *Synergus connatus* Hartig, 1840.

Body from entirely black to yellowish or light brown. Head delicately coriaceous to alutaceous, nearly as high as broad in front view; gena not broadened behind eye; malar space nearly 2.0 times shorter than height of eye, with striae radiating from clypeus and reaching eye margin; lower face coriaceous, with striae radiating from clypeus and reaching eye and antennal sockets and often extending into area between antennal socket and inner margin of eye; median elevated area coriaceous. Clypeus small, with indistinct tentorial pits, clypeo-pleurostomal line and epistomal sulcus indistinct; ventrally projecting over mandibles, widely emarginated, incised or not medially, rounded or straight. POL much longer than OOL; OOL always longer than diameter of lateral ocellus. Transfacial distance shorter than height of eye. Inner margins of eyes parallel or slightly converging ventrally. Frons delicately coriaceous, lateral frontal carina absent or very indistinct; vertex and occiput delicately coriaceous. Antennae 13–14-segmented in female, 14–15-segmented in males; F1 in males curved in middle and slightly expanded apically. Mesosoma flattened dorso-ventrally, longer than high in lateral view. Pronotum uniformly delicately coriaceous; lateral pronotal carina absent or present, corners of pronotum dorsally rounded or strongly angled. Scutum with delicate interrupted transverse striae. Notauli incomplete or complete; median scutal line absent or in a form of a short triangle. Scutellum slightly elongated or rounded, uniformly rugose; slightly overhanging metanotum. Scutellar foveae small, transverse, separated by central carina. Mesopleuron striate, metapleural sulcus reaching mesopleuron in upper 1/3 of its height, Lateral propodeal carinae uniformly broad, straight, subparallel or slightly converging inwards ventrally; central propodeal area coriaceous, with white setae in anterior half; lateral propodeal area delicately uniformly coriaceous, with relatively dense white setae. Forewing longer than body, margin with short cilia; radial cell opened along wing margin. Metasoma equal or slightly longer than head+mesosoma; metasomal tergites 2 and 3 fused, without punctures, with few white setae antero-laterally; hypopygium with dense punctures, prominent part of ventral spine of hypopygium very short, with few short white setae (Figs 3–5).



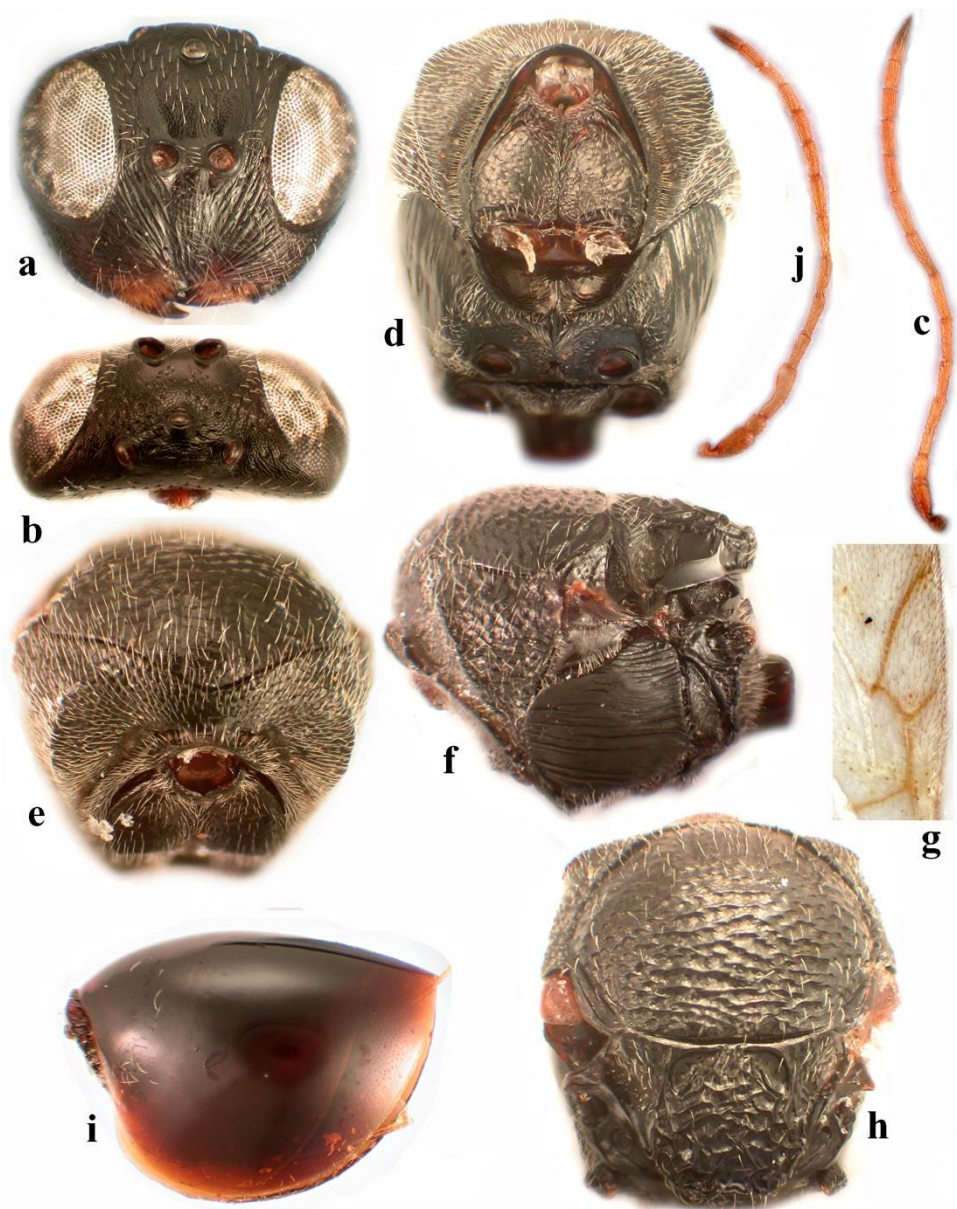


Figure 3. *Saphonecrus undulatus* (“undulatus” group): a–i, female: a, head, anterior view, b, head, dorsal view, c, antenna, d, mesosoma and propleura, anterior view, e, mesosoma, anterodorsal view, f, mesosoma, lateral view, g, forewing, part with radial cell, h, mesosoma, dorsal view, i, metasoma, lateral view. j, antenna, male.

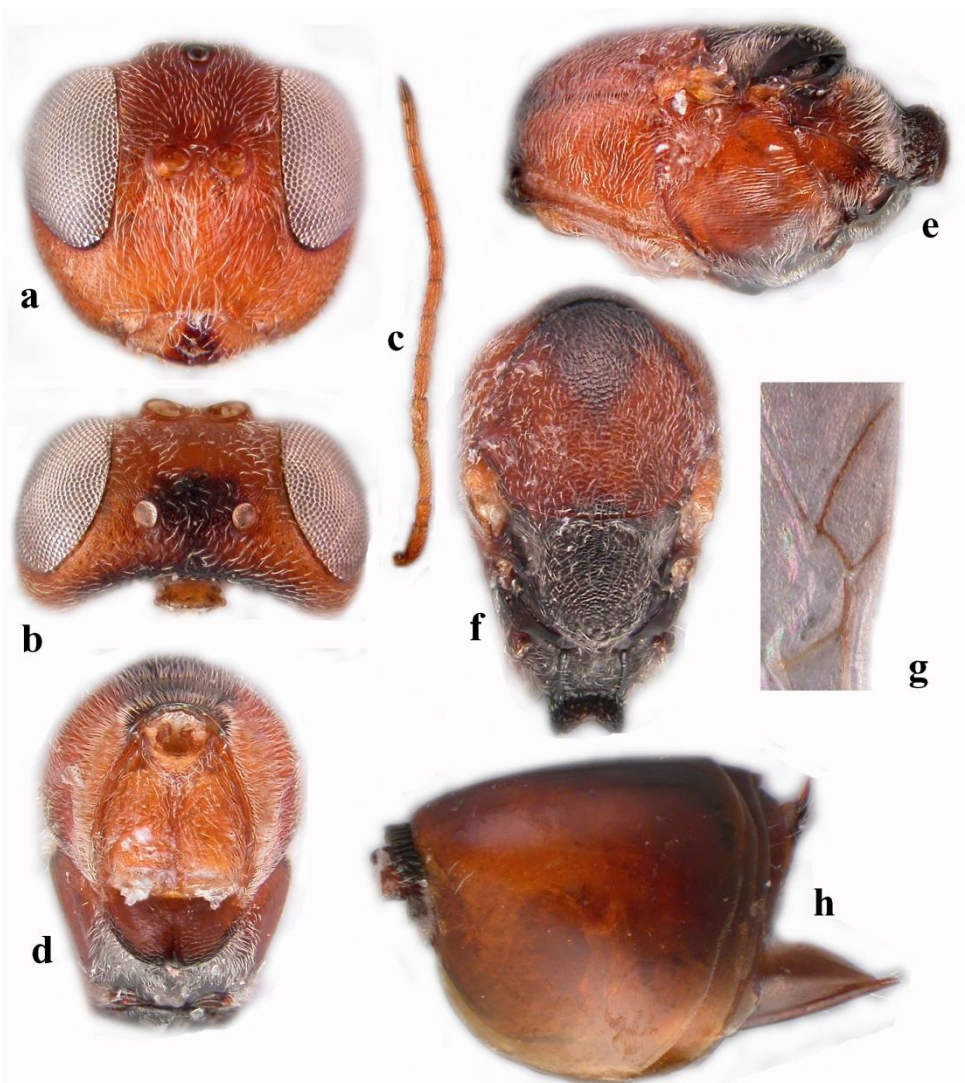


Figure 4. *Saphonecrus gallaepomiformis* (“barbotini” group), female: a, head, anterior view, b, head, dorsal view, c, antenna, d, mesosoma and propleura, anterior view, e, mesosoma, lateral view, f, mesosoma, dorsal view, g, forewing, part with radial cell, h, metasoma, lateral view.

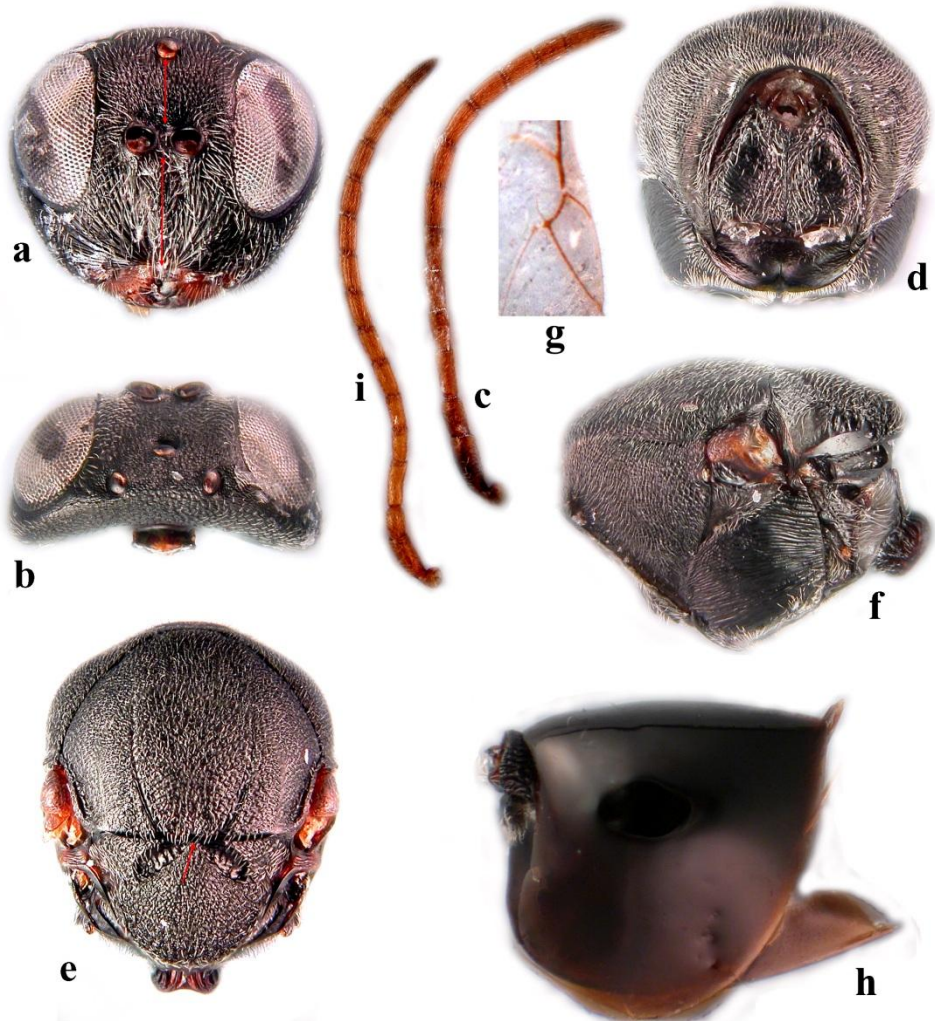


Figure 5. *Saphonecrus* “sp.50-51” (“connatus” group): a–h, female: a, head, anterior view, b, head, dorsal view, c, antenna, d, mesosoma and propleura, anterior view, e, mesosoma, dorsal view, f, mesosoma, lateral view, g, forewing, part with radial cell, h, metasoma, lateral view. i, antenna, male.

The genus *Saphonecrus* was established by Dalla Torre and Kieffer (1910) for the oak inquiline species with an open radial cell (in contrast to *Synergus*, where this cell is closed, except in *Synergus plagiotrochi*). Although the separation of this genus from *Synergus* has subsequently been widely questioned (Eady and Quinlan 1963, Ritchie 1984, Pujade-Villar and Nieves-Aldrey 1990), the two genera have never been formally synonymised. Ritchie (1984) regarded the characters distinguishing *Saphonecrus* from *Synergus* as apomorphic, and saw

*Saphonecrus* as a specialised monophyletic lineage within *Synergus*. Pujade-Villar and Nieves-Aldrey (1990) revised the European species and maintained the genus, but also questioned its validity. We consider *Saphonecrus* to be polyphyletic and closely allied to *Synergus*. The two genera can be separated by a combination of characters: *Saphonecrus* species have an open radial cell, female antennae have 13 segments, and the lateral frontal carinae usually are absent. In contrast, most *Synergus* species have a closed radial cell; female antennae are 14 segmented and lateral frontal carinae are usually present. The presence/absence of the lateral frontal carinae and lateral pronotal carina in *Saphonecrus* (*Synergus*) are inconsistent character states which about we shall talk in details later.

The Western Palaearctic species are associated mainly with galls on section Cerris oaks, including Mediterranean evergreen species (*Q. ilex*, *Q. suber*, *Q. coccifera*) and *Q. cerris* in Central Europe, while some are associated with galls develop on white oaks (e.g. *Q. petraea*, *Q. robur*). Species associated with Cerris and Quercus section oaks have a single generation per year and emerge after one winter in the gall, while those on evergreen oaks have at least the potential for two generations in a year (Pujade-Villar and Nieves-Aldrey 1990). It was showed that the biology of the European *Saphonecrus* species can be divided into three groups: (i) includes species with one annual generation, and associated with galls on section Quercus oaks (*S. connatus*); (ii) also includes monovoltine species, associated with galls on section Cerris oaks (*S. undulatus* and *S. haimi*; also *S. irani* belongs to this group); (iii) some Mediterranean species, with bivoltine life cycles, associated with galls on evergreen oaks (*S. barbotini* and *S. gallaepomiformis*) (Pujade-Villar and Nieves-Aldrey 1990). Pujade-Villar (2004) showed that the widely reported *Synergus gallaepomiformis* is a *Saphonecrus*, the senior synonym of *S. lusitanicus*, valid name of which must be *Saphonecrus gallaepomiformis* (Boyer de Fonscolombe, 1832). We follow this nomenclatorial change in our review.

*Saphonecrus* is distributed mainly in the Holarctic: six valid species are known for the Western Palaearctic, with a few uncertain status species (Pujade-Villar *et al.* 2003); 7 species were listed for the Eastern Palaearctic (Abe *et al.* 2007); 4 species for the Nearctic (Burks 1979), and only two species were known from the Oriental region (Weld 1926). Recently new species were described from Japan (Wachi *et al.* 2011a) and eastern palaeartic/oriental China (Wang *et al.* 2010). The first inquiline, *Saphonecrus hupingshanensis*, which associate with non-oak plant, *Castanopsis carlesii*, reared from a multi-chambered, midrib leaf gall, was described (Liu *et al.* 2012). Recently two *Andricus* Hartig species were transferred to *Ufo*, *U. shirakashii* (Shinji) and *U. shirokashicola* (Shinji) (Wachi *et al.* 2011b), however, genetic distances and morphological analyses showed that they are *Saphonecrus*, *S. shirakashii* and *S. shirokashicola* (Melika *et al.* 2012). A large number of new *Saphonecrus* and near *Saphonecrus* (new genera) species are under description. One species, *S. connatus*, thought to be a trans-palaeartic

species and was mentioned for Japan and Korea, reared from leaf galls on *Q. dentata* (Sakagami 1949, Abe *et al.* 2007). However, this record might be well *S. chaodongzhui* Melika, Ács & Bechtold known from China, which closely resembles *S. connatus* (Melika *et al.* 2004). Thus, the total number of known valid species of *Saphonecrus* is 23 (Table 5).

Two *Saphonecrus* species, *S. serratus* and *S. areolatus*, were described from Philippines (Weld 1926). The analyses of the types showed that both species have an unusually short pronotum dorsally, like in Cynipini. The head is transverse from above; the frons with strong parallel striae radiating from toruli and reaching ocelli and vertex; the radial cell of the forewing is opened, the forewing margin with long dense cilia; lateral propodeal carinae are curved outwards, not parallel; the last visible metasomal tergite with micropunctures, the prominent part the ventral spine of the hypopygium much longer than usually in *Saphonecrus*. At the same time, in *S. serratus* the female antenna with 13 flagellomeres and the 2<sup>nd</sup> metasomal tergite dorsally is not incised, straight; the metanotal trough without setae, glabrous, while in *S. areolatus* the female antenna with 12 flagellomeres and the 2<sup>nd</sup> metasomal tergite dorsally is strongly incised; the metanotal trough with dense white setae. These two species, definitely form a distinct unit, away from the typical *Saphonecrus* [detailed morphoanalysis and nomenclatorial changes concerning these two species will be done elsewhere].

Four Nearctic *Saphonecrus* species are known (Table 5), however, some of them possess some non-typical character states for *Saphonecrus* and produce a mixture of character states for *Saphonecrus-Synergus* and thus their assignment to *Saphonecrus* genus must be examined in details.

*Saphonecrus brevis* is known from New Mexico and Arizona, reared from stem swelling-like galls of *Andricus ruginosus* Bassett associated with white oaks. This species is similar to the European *Synergus plagiostrochi* with its opened radial cell in the forewing. Female antenna with 12 flagellomeres; lateral frontal carinae are absent; the mesoscutum with strong transverse shiny rugae, space between rugae shiny; notauli complete, reaching pronotum; lateral pronotal carinae are absent, thus the pronotum laterodorsally is rounded; the mesopleural sulcus nearly straight, do not bented towards the mesopleuron as in typical *Saphonecrus*; tarsal claws are simple. The last visible tergite dorsally microreticulate, not punctured as in other species of *Saphonecrus* and *Synergus*; the metasomal petiole with very weak, delicate striae laterally, no striae dorsally and the striae are not longitudinally orientated. So, *S. brevis* is not a “typical” *Saphonecrus* and might well represent a distinct genus.

*Saphonecrus brevicornis* based on the original description might be a good *Saphonecrus* (Ashmead 1896b).

Table 5. Known species of *Saphonecrus*: distribution and host associations.

Species	Distribution	Host plants
<i>S. areolatus</i> Weld, 1926	O: Philippines, Luzon	Unknown
<i>S. barbotini</i> Pujade-Villar & Nieves-Aldrey, 1985	WP: Iberia	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. brevicornis</i> (Ashmead, 1896)	NA: California	Unknown
<i>S. brevis</i> Weld, 1926	NA: USA, Arizona, New Mexico	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. chaodongzhui</i> Melika, Ács & Bechtold, 2004	EP: China, Yunnan	Unknown
<i>S. connatus</i> (Hartig, 1840)	WP: Europe	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. diversus</i> Belizin, 1968	EP: Russia, Primorskij Kraj	Unknown
<i>S. excisus</i> (Kieffer, 1904)	EP: Bengal, Kurseong	<i>Lithocarpus elegans</i>
<i>S. favanus</i> Weld, 1944	NA: DC and Missouri	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. flavitibialis</i> Wang & Chen, 2010	EP: China, Zhejiang	Unknown
<i>S. gemmariae</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. haimi</i> (Mayr, 1872)	WP: Europe, N.Africa	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. hupingshanensis</i> Liu, Yang & Zhu, 2012	EP/O: China, Hunan	<i>Castanopsis carlesii</i>
<i>S. irani</i> Melika & Pujade-Villar, 2006	WP: Iran	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. gallaepomiformis</i> (Boyer de Fonscolombe, 1832)*	WP: Iberia	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. naiquantini</i> Melika, Ács & Bechtold, 2004	EP: China, Zhejiang	Unknown
<i>S. serratus</i> Weld, 1926	O: Philippines, Luzon	Unknown
<i>S. shirakashii</i> (Shinji, 1940)	EP: Japan	<i>Quercus</i> subgenus <i>Cyclobalanopsis</i>
<i>S. shirokashicola</i> (Shinji, 1941)	EP: Japan	<i>Quercus</i> subgenus <i>Cyclobalanopsis</i>
<i>S. sinicus</i> Belizin, 1968	EP: China, Sichuan	Unknown
<i>S. tianmushanus</i> Wang & Chen, 2010	EP: China, Zhejiang	Unknown
<i>S. undulatus</i> (Mayr, 1872)	WP: Europe	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. yukawai</i> Wachi, Ide & Abe, 2011	EP: Japan	<i>Quercus</i> sect. <i>Cerris</i>
<b>Total: 23 species</b>		

\* earlier, in all relevant literature, this species was referred to *Saphonecrus lusitanicus* (Tavares, 1902). After examination of types, Pujade-Villar (2004) made the adequate nomenclatorial changes and proposed the new name, *Saphonecrus gallaepomiformis*, which we follow herein.

*Saphonecrus gemmariae* was described from Florida, on the basis of one male which emerged from *Callirhytis quercusgemmariae* (Ashmead) gall on red oaks (Ashmead 1885). The type supposed to be deposited at the Smithsonian Institution, USNM, however, was not located in the collection by the curator, M. Buffington and also by GM. The description of the male is very brief, not enough to make a definite decision whether *S. gemmariae* is really a *Saphonecrus* and thus must be treated as a species with uncertain status.

*Saphonecrus favanus* is known from the United States (DC and Missouri), reared from a root gall of *Dryocosmus favus* Beutenmüller on red oaks (Weld 1944). Morphologically a non-typical *Saphonecrus* species: the frons, vertex and mesoscutum with deep numerous punctures (somehow resembles *Synergus subterraneus*); the head quadrangular in front view, the clypeus impressed, the lower face delicately coriaceous, without radiating striae; female antenna with 11 flagellomeres; lateral frontal and lateral pronotal carinae are absent; the forewing without cilia; the metapleural sulcus reaches metapleuron in the upper 1/3 of its height; the petiole with parallel sulci all around; the last metasomal tergite posterodorsally with micropunctures posterodorsally. So, *S. favanus* is not a “typical” *Saphonecrus* and might well represent a distinct genus.

An ongoing research on Taiwan (T.C-T, GM) reveals a large number of new *Saphonecrus* and near *Saphonecrus* species, reared from different galls, what suggests that *Saphonecrus* is definitely a polyphyletic group and evolutionary relationships within this group are much more complicated that were thought earlier (Pérez *et al.* 2009, Ács *et al.* 2010). Description of new species and new genera are under preparation, a preliminary demonstration of diversity is illustrated below.

### ***Synergus* Hartig, 1840**

Type species: *Synergus vulgaris* Hartig, 1840.

Body length 0.8-4.5 mm, with sparse white setae. Predominantly black, chestnut brown or orange brown, antenna and legs always much lighter than body. Wing veins dark to pale brown. Head alutaceous to dull rugose, transverse in front view, with sparse white setae, nearly 2.0 times as broad as long from above and always broader than high in front view, slightly broader than mesosoma. Gena coriaceous, not broadened behind eye, invisible in front view behind eye, converging ventrally. Malar space nearly 2.0 times shorter than height of eye, with striae radiating from clypeus and reaching eye. POL around 2.0 times as long as OOL. Transfacial distance longer than height of eye. Lower face with more or less strong striae radiating from ventral margin of clypeus and usually reaching eye and antennal sockets. Clypeus with radiating striae, delimited from lower face by distinct anterior tentorial pits, epistomal sulcus and clypeo-pleurostomal line; ventrally usually straight. Frons coriaceous to dull rugose, with or without punctures; lateral frontal carinae strong or delicate, indistinct. Vertex and occiput dull rugose to delicately coriaceous, with or without punctures. Antennae 14–segmented in female and 15–segmented in male; F1 in male straight or modified, excavated and curved medially, broadened apically and/or basally. Mesosoma flattened dorso-ventrally, slightly longer

than high in lateral view, with white setae. Pronotum coriaceous to rugose, with white setae, lateral pronotal carina strong or absent, lateral corners of pronotum strongly angled or rounded. Scutum with or without transverse rugae, but always distinctly with transversely orientated sculpture. Notauli complete, deeply impressed or indistinct, incomplete, shallowly impressed; median mesoscutal line extending to half or more length of scutum or present in a form of short triangle only. Scutellum rounded, dull rugose to delicately coriaceous, slightly overhanging metanotum. Scutellar foveae present, separated by a more or less broad central carina. Mesopleuron striate. Metapleural sulcus reaching mesopleuron in upper one-third of its height. Lateral propodeal carinae nearly straight, subparallel or slightly converging inwards in the most posterior part. Forewing margin with cilia; radial cell closed, except partially closed in *S. plagiotrochi*. Metasomal tergites 2+3 fused, with more or less broad band of punctures posteriorly; prominent part of ventral spine of hypopygium very short (Fig. 6).

Mayr (1872) subdivided *Synergus* into two sections: Section I contains those species in which fused metasomal tergites 2+3 are with a more or less broad band of punctures posteriorly and Section II contains species in which fused metasomal tergites 2+3 have only a small dorso-posterior patch of punctures. This division is artificial and does not reflect the phylogenetic relationships (Ács *et al.* 2010), however, it was useful for the separation and classification of the species. Though initially proposed on the basis of morphology, these sections are also associated with apparent biological differences. Section I species predominantly have a single generation per year (univoltine), and their development in a host gall is rarely lethal to the gall-inducer. In contrast, Section II species predominantly have two generations per year (bivoltine), and their attack frequently causes death of the gall inducer (Csóka *et al.* 2005). Section II species are also characterised by high between-generation variation in some adult morphological attributes, particularly size and colour (Nieves-Aldrey and Pujade-Villar 1986, Pujade-Villar 1992, Wiebes-Rijks 1979), which can make morphology-based identification difficult. As a result, morphology-based identification is often only possible to complexes of morphologically similar species (Ács *et al.* 2010).

Many nearctic *Synergus* species differs from Palaearctic species by a simple tarsal claw and partially smooth, incompletely sulcated first tergite while in all Palaearctic species the tarsal claws possess a basal lobe and the first metasomal tergite is completely sulcate. It was already showed for *S. mexicanus* and *S. castanopsidis* (Pujade-Villar and Melika 2005). Preliminary morphological analyses showed that there are at least three distinct morphological groups within the nearctic *Synergus*, one of them does agree with the Palaearctic *Synergus* while two others are distinct. Further research will definitely split the current *Synergus* into a number of lineages as it was already found in *Saphonecrus*.



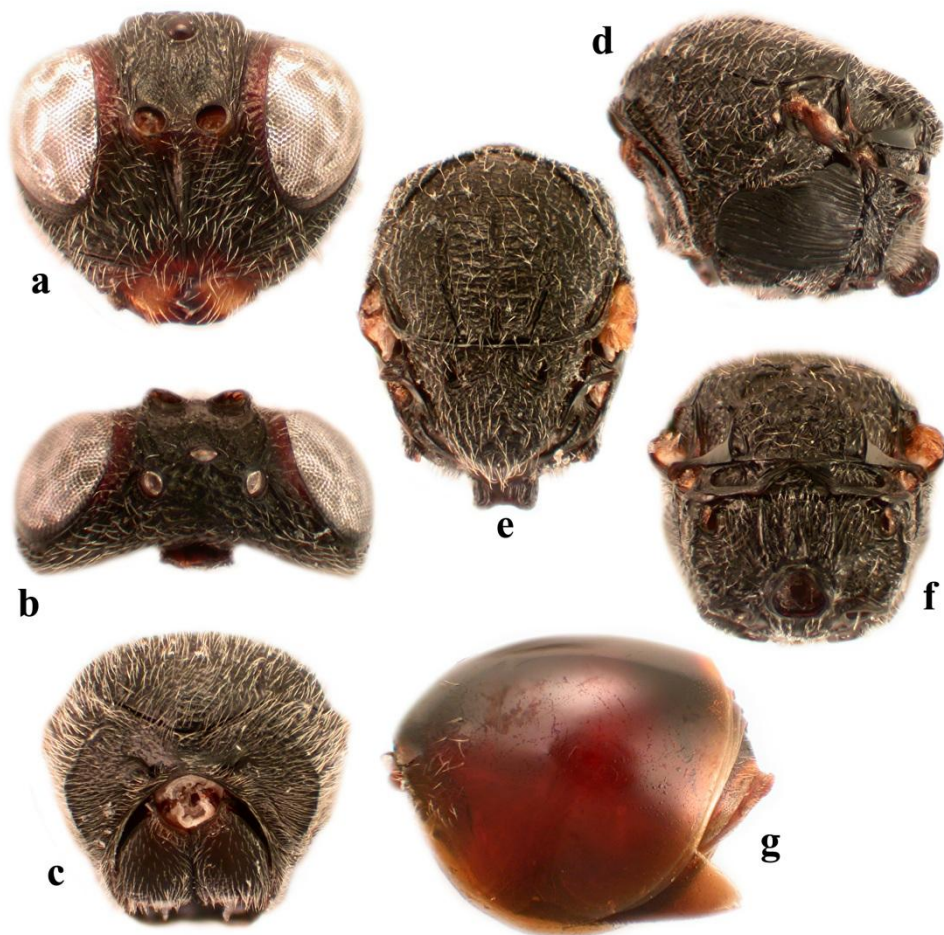


Figure 6. *Synergus facialis*, female: a, head, anterior view, b, head, dorsal view, c, mesosoma, anterodorsal view, e, mesosoma, dorsal view, d, mesosoma, lateral view, e, mesosoma, dorsal view, f, mesosoma and propodeum, anterodorsal view, g, metasoma, lateral view.

Pujade-Villar (2004) showed that the widely reported *Synergus gallaepomiformis* should be named *Synergus facialis* Hartig, 1840, and *Synergus gallaepomiformis* is a senior synonym of *Saphonecrus lusitanicus* and thus the valid name for the later must be *Saphonecrus gallaepomiformis* (Boyer de Fonscolombe, 1832). *Synergus facialis* (earlier widely referred as *S. gallaepomiformis*) has been reared from galls of *Andricus symbioticus* Kovalev and *A. attractus* Kovalev collected from *Q. mongolicus*, near Lake Khasan (Primorskij Kraj, Russia) (Kovalev 1965) which, however, we strongly doubt and

probably it is *S. chinensis* or an undescribed species, morphologically very similar to *S. facialis* (Abe *et al.* 2007).

*Synergus* is the most species-rich oak gall inquiline cynipid genus, with 109 known species (Table 6), with a long and complex history of taxonomic revision (see Pujade-Villar *et al.* 2003, Melika 2006). *Synergus* has mainly a Holarctic distribution, however, some species are known from the Oriental China and also from the Neotropical region. Currently 40 valid species are known from the Palaearctic: 30 from the Western Palaearctic (Pujade-Villar *et al.* 2003, Sadeghi *et al.* 2006); 10 from the Eastern Palaearctic (Table 6). Status of some Eastern Palaearctic species, described in the first half of 20th century, *S. atamiensis*, *S. hakonensis*, *S. iwatensis*, *S. jezoensis*, *S. mizunarae*, is still uncertain and must be solved (Abe *et al.* 2007).

Fifty five *Synergus* species are known from the Nearctic, 54 from America north of Mexico (USA and Canada) (Table 6). The fauna of Mexico is thought to be rich in inquiline species, though only two species have been actually recorded: *Synergus dugesi* and *S. filicornis* (syn. *S. furnessana*), known from the neotropical part of Mexico only and from Guatemala (Asmead 1899, Ritchie 1984, Ritchie and Shorthouse 1987a).

The inquiline oak gallwasp fauna of the Neotropics have been poorly studied and only representatives of *Synergus* genus are known for this region (Weld 1952, Ritchie and Shorthouse 1987a, Nieves-Aldrey 2005, Pujade-Villar and Hanson 2006). However, the distribution range of the host plant, *Quercus* and particularly section Lobatae, extends as far south as Colombia (Correa *et al.* 2004). *Synergus filicornis* described from Guatemala was for a long time the only *Synergus* recorded from Central and South America (Cameron 1883). Later, five species were added: *Synergus cultratus*, *S. mesoamericanus*, and *S. kinseyi* (Ritchie and Shorthouse 1987a) from Guatemala and *Synergus nicaraguensis* from Nicaragua (Díaz and Gallardo 1998). The southernmost American record for an oak cynipid inquiline was the recently described *Synergus colombianus* from Colombia (Nieves-Aldrey 2005). Other 8 species were recently described from Panama (Nieves-Aldrey and Medianero 2011). One species, *S. filicornis*, described from Guatemala, is known also from Mexico and originally was described by Weld (1913) as *S. furnessana*, however, later was synonymized to *S. filicornis* (Weld 1930). Thus, currently 14 *Synergus* species are known from the Neotropics (Table 6).

Table 6. Known species of *Synergus*: distribution and host associations.

<b>Species</b>	<b>Distribution</b>	<b>Host plants</b>
<i>S. acsi</i> Melika & Pujade-Villar, 2006	WP: Iran	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. agrifoliae</i> Ashmead, 1896	NA: USA, California	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. apicalis</i> Hartig, 1841	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. atamiensis</i> Ashmead, 1904	EP: Japan	Unknown
<i>S. atra</i> Gillette, 1896	NA: USA, Colorado	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. atripennis</i> Ashmead, 1896	NA: USA, Florida	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. atripes</i> Gillette, 1896	NA: USA, Colorado	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. baruensis</i> Nieves-Aldrey & Medianero, 2011	NT: Panama	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. batatoides</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. bechtoldae</i> Melika & Pujade-Villar, 2006	WP: Iran	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. bellus</i> McCracken & Egbert, 1922	NA: USA, California	Unknown
<i>S. bicolor</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. campanula</i> Osten Sacken, 1865	NA: Eastern USA	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. castanopsidis</i> (Beutenmüller, 1918)	NA: USA, California	<i>Chrysolepis</i> spp.
<i>S. chinensis</i> Melika, Acs & Bechtold, 2004	EP: China, Korea	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. chiricanus</i> Nieves-Aldrey & Medianero, 2011	NT: Panama	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. citriformis</i> (Ashmead, 1885)	NA: USA, Florida	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. clandestinus</i> Eady, 1952	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. colombianus</i> Nieves-Aldrey, 2005	NT: Colombia	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. confertus</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. coniferae</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. consobrinus</i> Giraud in Houard, 1911	WP: Austria, Hungary	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. crassicornis</i> (Curtis, 1838)	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. cultratus</i> Ritchie & Shorthouse, 1987	NT: Guatemala	<i>Quercus</i> sect. <i>Quercus</i>

<i>S. dacianus</i> Kierych, 1985	WP: Europe	<i>Quercus</i> sect. Cerris
<i>S. davisii</i> (Beutenmüller, 1907)	NA: USA, New Jersey	<i>Quercus</i> sect. Lobatae
<i>S. diaphanus</i> Houard, 1911	WP: Austria, Hungary	<i>Quercus</i> sect. Quercus
<i>S. digressus</i> McCracken & Egbert, 1922	NA: USA, California	Unknown
<i>S. dimorphus</i> Osten Sacken, 1865	NA: USA, DC	Unknown
<i>S. distinctus</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. Quercus
<i>S. dorsalis</i> (Provancher, 1888)	NA: USA, California	Unknown
<i>S. dugesi</i> Ashmead, 1899	NA: Mexico	<i>Quercus</i> sect. Quercus
<i>S. duricoria</i> Gillette, 1896	NA: USA, Delaware	<i>Quercus</i> sect. Quercus
<i>S. elegans</i> Nieves-Aldrey & Medianero, 2011	NT: Panama	<i>Quercus</i> sect. Quercus and Lobatae
<i>S. erinacei</i> Gillette, 1896	NA: USA, NY, Iowa	Unknown
<i>S. facialis</i> Hartig, 1840*	WP: throughout	<i>Quercus</i> sect. Quercus
<i>S. ficigeræ</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. Quercus
<i>S. filicornis</i> Cameron, 1883	NT: Guatemala	<i>Quercus</i> sect. Quercus
<i>S. flavens</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. Protobalanus
<i>S. flavipes</i> Hartig, 1843	WP: Austria, Hungary	<i>Quercus</i> sect. Cerris
<i>S. flavus</i> Kieffer, 1904	NA: USA, California	<i>Quercus</i> sect. Lobatae
<i>S. gabrieli</i> Nieves-Aldrey & Medianero, 2011	NT: Panama	<i>Quercus</i> sect. Lobatae
<i>S. garryana</i> Gillette, 1893	NA: USA, Wash., Oregon	<i>Quercus</i> sect. Quercus
<i>S. gifuensis</i> Ashmead, 1904	EP: Japan	<i>Quercus</i> sect. Quercus
<i>S. hakonensis</i> Ashmead, 1904	EP: Japan	Unknown
<i>S. hayneanus</i> (Ratzeburg, 1833)	WP: throughout	<i>Quercus</i> sect. Quercus
<i>S. ibericus</i> Tavares, 1920	WP: Iberian Peninsula	<i>Quercus</i> sect. Quercus
<i>S. ilicinus</i> (Barbotin, 1972)	WP: Spain, France	<i>Quercus</i> sect. Cerris
<i>S. incisus</i> Gillette, 1896	NA: USA, Colorado	<i>Quercus</i> sect. Quercus
<i>S. incrassatus</i> Hartig, 1840	WP: throughout	<i>Quercus</i> sect. Quercus
<i>S. itoensis</i> Abe, Ide & Wachi, 2011	EP: Japan	<i>Quercus</i> subgenus <i>Cyclobalanopsis</i>

<i>S. iwatensis</i> Shinji, 1941	EP: Japan	Unknown
<i>S. japonicus</i> Walker, 1874	EP: Japan, Korea	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. jezoensis</i> Uchida & Sakagami, 1948	EP: Japan	Unknown
<i>S. kinseyi</i> Ritchie & Shorthouse, 1987	NT: Guatemala	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. laeiventris</i> (Osten Sacken, 1861)	NA: USA, DC	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. laticephalus</i> Nieves-Aldrey & Medianero, 2011	NT: Panama	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. lignicola</i> (Osten Sacken, 1862)	NA: Eastern USA	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. luteus</i> Nieves-Aldrey & Medianero, 2011	NT: Panama	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. magnificus</i> Weld, 1957	NA: USA, California	<i>Quercus</i> sect. <i>Protobalanus</i>
<i>S. magnus</i> Gillette, 1891	NA: USA, Michigan	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. medullae</i> Ashmead, 1885	NA: USA, Florida	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. mendax</i> Walsh, 1864	NA: USA, Illinois	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. mesoamericanus</i> Ritchie & Shorthouse, 1987	NT: Guatemala, Panama	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. mexicanus</i> Gillette, 1896	NA: USA, New Mexico	Unknown
<i>S. mikoi</i> Melika & Pujade-Villar, 2006	WP: Iran	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. mizunarae</i> Shinji, 1940	EP: Japan	Unknown
<i>S. multiplicatus</i> Fullaway, 1911	NA: USA, California	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. nicaraguensis</i> Díaz & Gallardo, 1998	NT: Nicaragua, Panama	<i>Quercus</i> sect. <i>Quercus</i> and <i>Lobatae</i>
<i>S. niger</i> Fullaway, 1911	NA: USA, California	Unknown
<i>S. nigroornatus</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. <i>Protobalanus</i>
<i>S. obtusilobae</i> (Ashmead, 1885)	NA: USA, Florida	Unknown
<i>S. ochreus</i> Fullaway, 1911	NA: USA, California	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. oneratus oneratus</i> (Harris, 1841)	NA: Eastern USA	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. oneratus coloradensis</i> Gillette, 1896	NA: USA, Colorado	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. pacificus</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. <i>Protobalanus</i>
<i>S. pallicornis</i> Hartig, 1841	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. pallidipennis</i> Mayr, 1872	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>

<i>S. pallipes</i> Hartig, 1840	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. palmirae</i> Melika & Pujade-Villar, 2006	WP: Iran	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. physocerus</i> Hartig, 1843	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i> and <i>Cerris</i>
<i>S. plagiostrochi</i> Nieves-Aldrey & Pujade-Villar, 1986	WP: Spain, France	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. pomiformis</i> (Ashmead, 1885)	NA: USA, California	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. profusus</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. punctatus</i> Gillette, 1896	NA: USA, Colorado	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. quercuslana</i> (Fitch, 1859)	NA: USA, NY, Iowa	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. radiatus</i> Mayr, 1872	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. ramoni</i> Nieves-Aldrey & Medianero, 2011	NT: Panama	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. reinhardi</i> Mayr, 1872	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. reniformis</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. <i>Protobalanus</i>
<i>S. ruficornis</i> Hartig, 1840	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. rufinotaulis</i> Nieves-Aldrey & Medianero, 2011	NT: Panama	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. rutulus</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. similis</i> Gillette, 1896	NA: USA, Colorado	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. splendidus</i> Fullaway, 1911	NA: USA, California	<i>Quercus</i> sect. <i>Lobatae</i>
<i>S. stelluli</i> Burnett, 1976	NA: USA, California	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. subterraneus</i> Giraud (in Houard, 1911)	WP: Austria, Spain	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. succinipedis</i> (Ashmead, 1885)	NA: USA, Florida	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. synophri</i> Kieffer, 1901	WP: North Africa	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. thaumacerus</i> (Dalman, 1823)	WP: throughout	<i>Quercus</i> sect. <i>Cerris</i> and <i>Quercus</i>
<i>S. tibialis</i> Hartig, 1840	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. umbraculus</i> (Olivier, 1791)	WP: throughout	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. variabilis</i> Mayr, 1872	WP: Europe	<i>Quercus</i> sect. <i>Cerris</i>
<i>S. varicolor</i> Fullaway, 1911	NA: USA, California	<i>Quercus</i> sect. <i>Lobatae</i>

<i>S. variegatus</i> McCracken & Egbert, 1922	NA: USA, California	<i>Quercus</i> sect. Protobalanus
<i>S. villosus</i> Gillette, 1891	NA: USA, Michigan	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. virentis</i> (Ashmead, 1885)	NA: USA, Florida	<i>Quercus</i> sect. <i>Quercus</i>
<i>S. walshii</i> Gillette, 1896	NA: USA, Illinois	Unknown
<i>S. xialongmeni</i> Melika, Ács & Bechtold, 2004	EP: China	<i>Quercus</i> sect. <i>Quercus</i>
<b>Total: 109 species</b>		

\* earlier known as *S. gallaepomifomis* (Boyer de Fonscolombe, 1832), after the examination of types, the valid name is *Synergus facialis* (Pujade-Villar 2004).

### ***Synophrus* Hartig, 1843**

Type species: *Synophrus politus* Hartig, 1843.

Morphologically, *Synophrus* appears most closely related to *Saphonecrus* (Melika 2006, Péntzes *et al.* 2009). Two morphological characters have been suggested to separate *Synophrus* from *Saphonecrus*: in *Synophrus* the metapleural sulcus reaches the anterior margin of the metapleuron at half or slightly higher of its height and the 2nd metasomal tergite has longitudinal sulci only laterally, being smooth dorsally, while in *Saphonecrus* the metapleural sulcus reaches the anterior margin of the metapleuron in the upper 1/3 of its height, and the entire 2nd metasomal tergite has longitudinal sulci (Pujade-Villar *et al.* 2003). In *Synophrus* lateral frontal carinae are absent; male antennae has 13 flagellomeres; lateral propodeal carinae are absent, the pronotum is rounded in dorsal view; the radial cell in the forewing is opened (Fig. 7) (Péntzes *et al.* 2009).

Currently 7 *Synophrus* species are known from the Western Palaearctic only (Table 7), all of which are able to impose their own gall phenotypes on those of their hosts (Péntzes *et al.* 2009).

One species, *Synophrus mexicanus* (Gillette, 1896) was listed for the nearctic fauna (Burks 1979). Originally it was described as a *Synergus* (Gillette 1896), later Weld (1952) transferred it to *Synophrus* and Ritchie (1984) affirmed that. Examination of the type verified that it is a *Synergus* species and thus its original status, *Synergus mexicanus*, was restored (Pujade-Villar and Melika 2005).

Weidner (1961) recorded *Synophrus olivieri* from the Indian Himalaya, but this identification is almost certainly incorrect.

Originally described as a gall inducer (Hartig 1843), *Synophrus* was later transferred to the Synergini on the basis of adult morphology (Ronquist 1994). An inquiline life history is supported by indirect evidence. It was observed that *S. politus* emerged from irregularly spherical and highly lignified stem swelling galls that developed over the summer in the exact location in which spring bud galls of a known gall inducing wasp, *Andricus burgundus* Giraud were initiated (Pujade-Villar *et al.* 2003). This modification of the host gall is extreme among cynipid inquelines, and attack by *Synophrus* is always lethal to the host gallwasp.

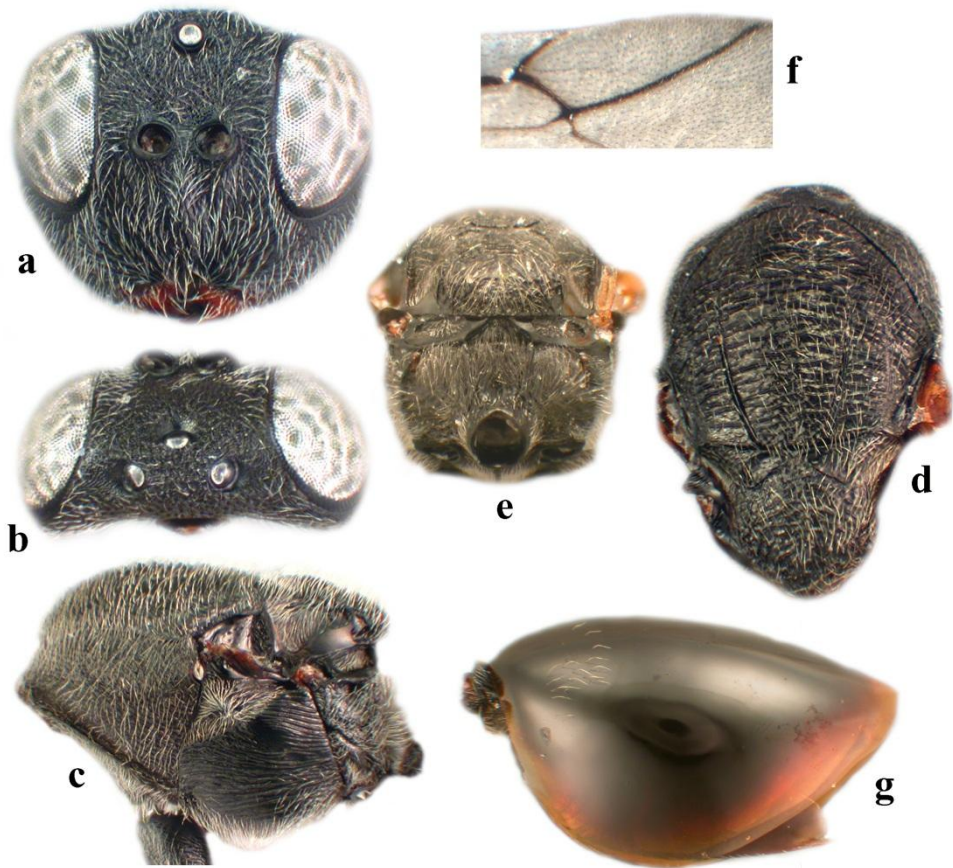


Figure 7. *Synophrus hungaricus*, female: a, head, anterior view, b, head, dorsal view, c, mesosoma, lateral view, e, mesosoma, dorsal view, d, mesosoma and propodeum, anterodorsal view, f, forewing, part with radial cell, g, metasoma, lateral view.

### ***Ufo* Melika & Pujade-Villar, 2005**

Type species: *Ufo abei* Melika et Pujade-Villar, 2005.

*Ufo* is characterized by the next morphological characters: head trapezoid (in females) or ovate (in males) in anterior view; strongly transverse, 2.5–2.8 times broader than high in dorsal view; frons and vertex alutaceous or smooth; intercellular triangle very narrow, posterior edge of frontal ocellus lies on line between anterior edges of lateral ocelli; occiput and postgena smooth; anterior part of pronotum rectangular in dorsal view, anterior and lateral sides form a right angle; pronotum descending vertically to propleura; lateral part of pronotum going down from dorsal part also nearly at a right angle; strong pronotal carina divides lateral part from frontal, both of which also oriented almost at right angle to each other; tarsal claws with distinct acute basal lobe (Fig. 8).



Table 7. Known species of *Synophrus*: distribution and host associations.

Species	Distribution	Host plants/galls
<i>S. hungaricus</i> Melika & Mikó, 2009	WP: Hungary	<i>Quercus</i> sect. Cerris
<i>S. libani</i> Melika & Pujade-Villar, 2009	WP: Lebanon	<i>Quercus</i> sect. Cerris
<i>S. olivieri</i> Kieffer, 1898	WP: N.Africa, Iran, Caucasus	<i>Quercus</i> sect. Cerris
<i>S. pilulae</i> Houard, 1911	WP: Austria, Hungary	<i>Quercus</i> sect. Cerris
<i>S. politus</i> Hartig, 1843	WP: Europe, Turkey, Jordan	<i>Quercus</i> sect. Cerris
<i>S. syriacus</i> Melika, 2009	WP: Iran, Syria	<i>Quercus</i> sect. Cerris
<i>S. hispanicus</i> Pujade-Villar, 2009	WP: Iberia	<i>Quercus</i> sect. Cerris
<b>Total: 7 species</b>		

In the allied genera, *Synergus* and *Saphonecrus*, the head is usually rounded, quadrangular or slightly ovate in anterior view; less transverse in dorsal view, only 1.6–2.1 times as broad as high; the frons and vertex always clearly sculptured, at least delicately coriaceous; interocellar triangle much broader; the occiput is sculptured; the lateral pronotal carina, when present, never with a rectangular aspect in dorsal view, the pronotum more rounded in dorsal view; the base of the tarsal claw is broadened, and the basal lobe present, however, not in a form of an acute lobe. Also the host plant associations for all *Ufo* species is typical – they always attack galls developing on *Quercus* section Cerris only (Melika *et al.* 2012).

Four species of *Ufo* are known, three from the Eastern Palaearctic and one from the Oriental Region (Table 8).

Table 8. Known species of *Ufo*: distribution and host associations.

Species	Distribution	Host plants/galls
<i>U. abei</i> Melika & Pujade-Villar, 2005	EP: Japan	<i>Quercus</i> sect. Cerris
<i>U. cerroneuroteri</i> Tang & Melika, 2012	OR: Taiwan	<i>Quercus</i> sect. Cerris
<i>U. koreanus</i> Melika, Pujade-Villar & Choi, 2007	EP: Korea	<i>Quercus</i> sect. Cerris
<i>U. nipponicus</i> Melika, 2012	EP: Japan	<i>Quercus</i> sect. Cerris
<b>Total: 4 species</b>		

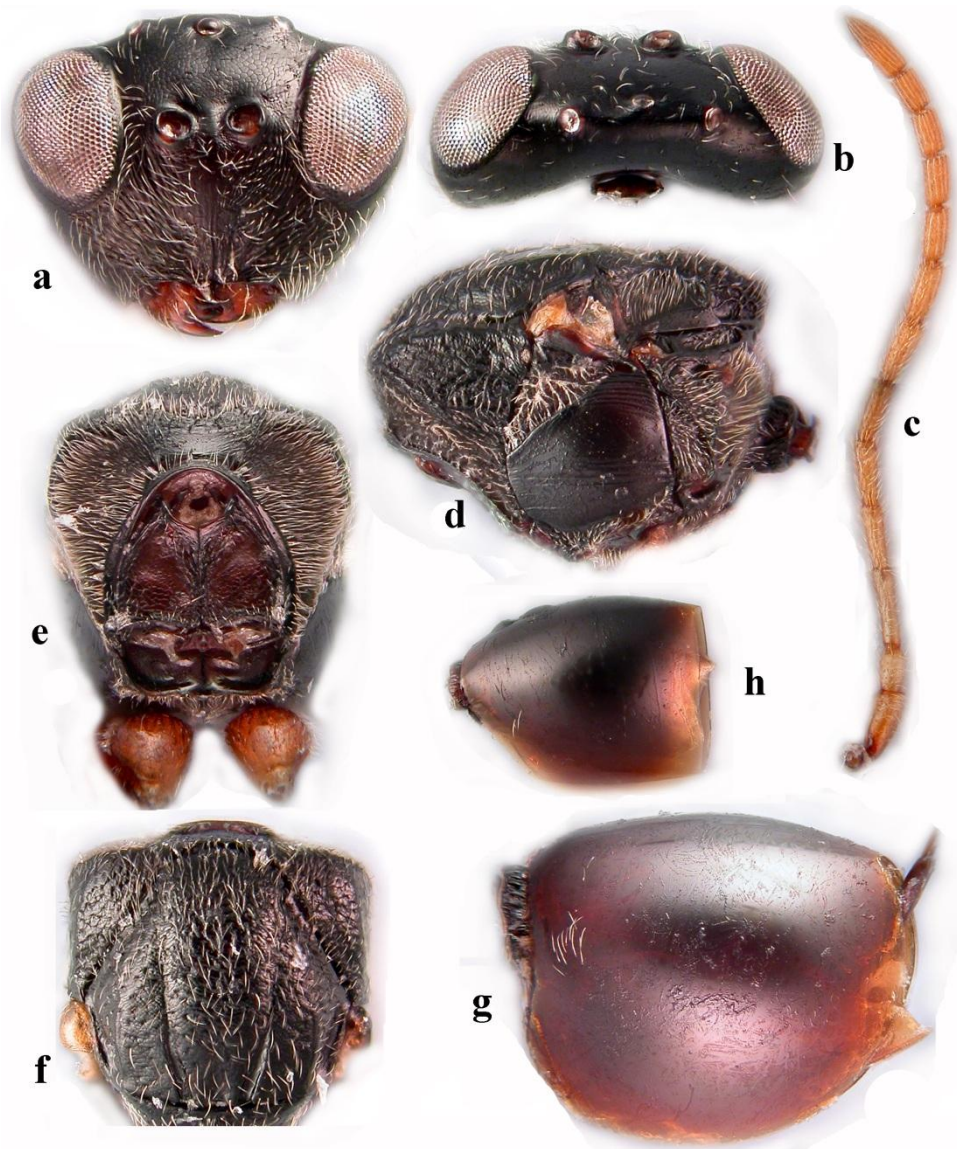


Figure 8. *Ufo cerroneuroteri*: a–g, female: a, head, anterior view, b, head, dorsal view, c, antenna, d, mesosoma, lateral view, e, mesosoma and propleura, anterior view, f, pronotum and mesoscutum, dorsal view, g, metasoma, lateral view. h, metasoma, lateral view, male.

Based on the morphology and DNA sequences, *Ufo* belongs to the Synergus complex of genera (Melika *et al.* 2005, 2007, 2012). Within the Synergus complex, *Ufo* possesses with a few synapomorphies: the head is trapezoid in

anterior view and very narrow in dorsal view, rectangular aspect of the pronotum has distinct rectangular aspect in dorsal view, the tarsal claw with a very acute basal lobe, host cynipid galls associated exclusively with oaks of subgenus *Quercus*, section *Cerris*. *Ufo* forms a distinct group within the *Synergus* complex as detailed below.

## Plant hosts of oak cynipid inquilines

Cynipid inquilines associate with gallwasps which are intimate parasites of oak trees, and in order to understand their evolution the knowledge of their host plant associations is important. Recent analyses primarily of Western Palaearctic oak gallwasps have revealed a deep phylogenetic divide between gallwasp taxa galling different oak sections (Cook *et al.* 2002, Ács *et al.* 2007, Liljeblad *et al.* 2008, Stone *et al.* 2009). A deep evolutionary split might be in host plant associations of inquilines, particularly those of the *Synergus* complex (Ács *et al.* 2010). The aim of this chapter is to provide an outline of taxonomy, diversity and distribution of oaks and oak related genera, to introduce briefly the phylogenetic and phylogeographic patterns in oaks and oak relatives and how they influence the phylogeny of cynipid inquilines.

Nine genera are recognised within the angiosperm family Fagaceae, which contains two highly diverse morphological groups that dominate a variety of habitats throughout the Northern Hemisphere. Fagaceae is divided into two subfamilies: Fagoidea, with *Fagus* and *Quercus* genera [the latter is a host plant for almost all known Cynipini] and Castaneoidea, with insect-pollinated *Castanea*, *Castanopsis*, *Chrysolepis*, *Lithocarpus* and *Notholithocarpus*, all five of which serve as hosts for Cynipini (Govaerts and Frodin 1998, Manos *et al.* 2008; Fig 9). The number of known species within Fagaceae is controversial; from 900 to *ca.* 1050 species are mentioned (Govaerts and Frodin 1998, Oh and Manos 2008). Several tropical close relatives of oaks have in the past been included in the genus *Quercus*, including the genus *Trigonobalanus* from Malaysia and Borneo, *Colombobalanus* from Colombia, and *Formanodendron* from China and southeastern Asia. These three genera have now been combined in the genus *Trigonobalanus* (Nixon and Crepet 1989, Govaerts and Frodin 1998), and though undoubtedly closely related to oaks, no gallwasps are known yet to gall *Trigonobalanus* species. The family Fagaceae also includes the southern beeches of the genus *Nothofagus*, with 36 known species distributed in South America (Chile and Argentina) and Australasia (Li *et al.* 2007). Though no Cynipini attack *Nothofagus*, they have been colonised by the gallwasp genera *Paraulax* Kieffer and *Cecinothofagus* Nieves-Aldrey & Liljeblad (tribe Paraulacini) documented in Chile and Argentina, however no Cynipidae are

known on this genus from Australasia (Nieves-Aldrey *et al.* 2009). Gallwasps have thus colonised the plant family Fagaceae at least twice.

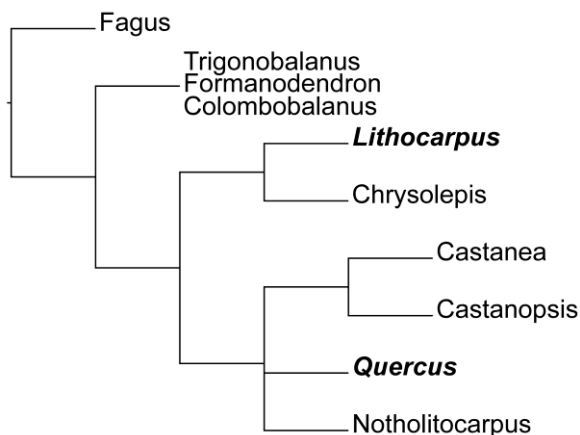


Figure 9. Phylogeny of Fagaceae (modified from Oh and Manos 2008)

*Castanea* (chestnuts) genus is represented by 8–10 species, native to temperate regions of the Northern Hemisphere, with only one known gallwasp, *Dryocosmus kuriphilus*. However, cynipid inquiline was not reared yet from these galls.

*Castanopsis* (chinquapin oaks) is a genus of evergreen trees which contains about 120 species, which are today restricted to tropical and subtropical eastern Asia (Oh and Manos 2008). Total of 58 species are native to China, with 30 endemic; the other species occur further south in Indochina to Indonesia, and also few species are known from Japan (<http://www.efloras.org/>). Recently a number of new gallwasp and cynipid inquiline species were described from *Castanopsis*.

*Chrysolepis* (golden chinquapin oaks) is a small genus, endemic to the western United States (from western Washington south to the Transverse Ranges in Southern California, and east into Nevada), with two species. *Ch. chrysophylla* and *Ch. sempervirens*. Some morphological features of the genus resemble those of *Castanopsis* but differ in the nuts being triangular and fully enclosed in a sectioned cupule, and in having bisexual catkins. The fruits somehow resemble nuts of *Castanea* (chestnuts), but in *Chrysolepis* nuts develop 14–16 months while in *Castanea* only 3–5 months and have evergreen leaves. Some inquiline wasps associate with few cynipid gallwasps develop on *Chrysolepis* species.

Manos *et al.* (2001) mentioned 334 species worldwide for *Lithocarpus* sensu stricto (stone oaks), others listed only 100 species or even less (Flora of Taiwan 1996). Earlier about 100 species were treated in *Pasania* genus (*e.g.* Flora of

Taiwan 1996) which was synonymized to *Lithocarpus* and currently all are treated together in *Lithocarpus* genus (Govaerts and Frodin 1998). All are native to east and southeast Asia. They are evergreen trees with leathery, alternate leaves, the seed is a nut very similar to an oak acorn, but with a very hard, woody nut shell. *Saphonecrus* inquiline associates with cynipid gallwasps develop on *Lithocarpus* species.

*Notholithocarpus* (tanbark oaks or tanoaks) with only one known North American species, *N. densiflorus*, only recently was established (Manos *et al.* 2008, Oh and Manos 2008). It is an evergreen tree, native to the western United States, California. It is most closely related to the north temperate oaks, *Quercus*, but not to the Asian *Lithocarpus*. Few cynipids are known to associate with this host.

Majority of Cynipini induce galls on members of a large, systematically well-studied, wind-pollinated genus *Quercus* which is divided into two long-established subgenera – the strictly Asian subgenus *Cyclobalanopsis* (the cycle cup or ring cup oaks), and the more widespread subgenus *Quercus* (Camus 1936-54, Nixon 1985, 1993, Govaerts and Frodin 1998, Manos *et al.* 1999).

The subgenus *Quercus* is divided into several discrete sections (Govaerts and Frodin 1998), including Lobatae (the red oaks), Protobalanus (the golden cup or intermediate oaks), *Quercus sensu stricto* (the white oaks), and Cerris. This classification is based on molecular phylogenies (Manos *et al.* 1999, Manos and Stanford 2001) and differs slightly from the alternatives based on morphological or biochemical traits (*e.g.* Nixon 1993, Zhou *et al.* 1995). The section Cerris has sometimes been divided into two subsections: *Ilex* species groups (with evergreen leaves) and Cerris species groups (with semi-deciduous leaves) (Nixon 1993). Of the 4 oak sections in the subgenus *Quercus*, *Quercus sensu stricto* is holarctic, Lobatae and Protobalanus are restricted to North America, and Cerris is restricted to the Palaeartic.

Worldwide, there are 531 recognised oak species (Govaerts and Frodin 1998). This total is divided between the Southeast Asian subgenus *Cyclobalanopsis* (76 species), and the more widespread subgenus *Quercus*, with 455 species. The subgenus *Quercus* is most abundant in temperate regions of the Northern Hemisphere. In the Neotropics oaks extend southwards as far as the Colombian Andes (Nieves-Aldrey 2005). In the Eastern Palaeartic, oaks, particularly *Cyclobalanopsis* species are a major component of climax forests in highland areas from the eastern Himalayas southwards through the Philippines and Malaysia into Java (Docters van Leuwen-Reijnvaan and Docters van Leuwen 1926).

Oak species richness is highest in the Nearctic (*ca.* 300 species) and the epicentre of modern oak richness is in the Sierra Madre Occidental of Mexico (*ca.* 135-200 species) (Nixon 1993, Manos *et al.* 1999). The Palaeartic supports *ca.* 170 species, with *ca.* 130 species in the Eastern Palaeartic and only 29 species in

the Western Palaearctic (Govaerts and Frodin 1998), with 13 in section *Cerris* and 16 in *Quercus sensu stricto*. The oak flora of the Western Palaearctic is clearly defined, and only one oak species from the Western Palaearctic, *Q. cerris*, is also recorded from western Afghanistan (Govaerts and Frodin 1998). The oak sections *Cerris* and *Quercus sensu stricto* are widespread in the Eastern Palaearctic, and the regional richness of oaks – with 32 species in China (Linkuo and Tao 1998), at least 17 in Himalayan India, Nepal and Bhutan (Negi and Naithani 1995), and 6 in Japan (Ohwi 1961) – exceeds the Western Palaearctic's 29 species.

The monophyly of two Fagaceae subfamilies, Castaneoideae and Fagoideae, were suggested by their remarkably similar flowers. However, recent phylogenetic reconstructions based on molecular data provide a strong evidence to reject the monophyly of the subfamily Castaneoideae and showed two distinct lineages within it (Manos *et al.* 2008, Oh and Manos 2008). Within this paraphyletic subfamily there are several well supported lineages. *Chrysolepis* is strongly supported as sister group to Asian species of *Lithocarpus*; while the North American *Notholithocarpus densiflorus* is placed within the *Quercus* and *Castanea* + *Castanopsis* clade, several nodes away from *Lithocarpus* (Fig. 9). Phylogenies of castaneoid genera also strongly supports *Castanea* and the strictly southeast Asian genus *Castanopsis* as sister taxa which agree with some molecular studies and taxonomic treatments (Camus 1936-54, Manos *et al.* 2001, Oh and Manos 2008).

Recent combined analysis resolved two clades of *Quercus* and *Quercus* subgenus *Quercus* was shown to be non-monophyletic. Oh and Manos (2008) recovered a mostly New World clade of species classified within subgenus *Quercus* representing the sections *Quercus s.str.* (white oaks), *Protobalanus*, and *Lobatae*. However, the Old World species classified within subgenus *Quercus* section *Cerris* are more closely related to *Quercus* subgenus *Cyclobalanopsis* than they are to other sections of subg. *Quercus*. The strictly Old World groups are united into one clade, and because the monophyly of the oaks remains likely, this novel pairing of temperate (sect. *Cerris*) and tropical (subg. *Cyclobalanopsis*) lineages suggests that previous classifications of the oaks was problematic (Oh and Manos 2008). More data are needed to resolve the placement of the two groups of *Quercus* relative to *N. densiflorus* and *Castanea* + *Castanopsis*.

Oaks and their close relatives probably first diversified in Southeast Asia, either during the Palaeocene (65–56 mya) or the Eocene (56–35 mya) (Zhou 1992, 1993, Cannon and Manos 2003, Manos *et al.* 1999), with an ancient divide into two monophyletic lineages: (i) the subgenus *Cyclobalanopsis* and the section *Cerris* of the subgenus *Quercus* and (ii) sections *Lobatae*, *Quercus sensu stricto* and *Protobalanus* of the subgenus *Quercus* (Manos and Stanford 2001). The Asian distribution of *Cyclobalanopsis*, the eurasian distribution of section *Cerris*, and the absence of fossils of these two groups from the Nearctic suggest that oaks originated and differentiated into these two basal lineages in Asia, but this

conclusion remains tentative (Zhou 1992, 1993, Manos and Stanford 2001). A striking feature of phylogenetic analyses of the oak gallwasps (Ács *et al.* 2007, Stone *et al.* 2009) is that (with the exception of host alternator species) they show the same deep divide between genera associated with section *Cerris* on one hand, and those associated with sections *Quercus sensu stricto* and the nearctic red oak section *Lobatae* on the other. If the divergence between the oak sections occurred in Eastern Asia, then it is plausible that this same region was the cradle for the origin and initial diversification of oak gallwasps and their inquilines.

After the initial diversification of oaks and oak relatives in Asia, one lineage dispersed into North America via the Bering Land bridge, which existed for long periods through the Eocene and Oligocene (38–25 mya) into the early Miocene (25–5 mya). Warmer global climates through the Eocene and early Oligocene allowed oak forests to develop across northeastern Siberia and across the Bering Land bridge into Alaska, Canada and Greenland (Thorne 1993, White *et al.* 1997, Zhou 1992, 1993). Oaks were present in North America from the Eocene (56–35 mya), and there gave rise to the oak sections *Lobatae*, *Protobalanus* and *Quercus sensu stricto*. Palaeartic white oaks were probably derived from ancestors that spread westwards from North America back across the Bering land bridge in the Oligocene (White *et al.* 1997, Manos and Stanford 2001), and the white oak floras of these two major regions have had separate evolutionary histories for *ca.* 17 mya (Manos and Stanford 2001). From early Asian centres of diversity, oaks in the sections *Cerris* and *Quercus sensu stricto* reached the Western Palaeartic by spreading westwards along the foothills of the Himalaya and the temperate highlands of Central Asia, and the western palaeartic radiations in both oak sections are thought to be relatively recent, dating from around the Pliocene (*ca.* 5mya) (Manos and Stanford 2001).

## Phylogeny of Synergini

Cynipoid wasps (Cynipoidea) are fall into two groups: macrocynipoids and microcynipoids (Ronquist 1995, 1999). The phytophagous gallwasps (gall inducers and inquilines, Cynipidae) are microcynipoids. During the last decade the Cynipoidea and particularly Cynipidae have been subject to intense phylogenetic research based on morphological characters of adults, gene sequences and gall structures (Cook *et al.* 2002, Liljeblad 2002, Liljeblad and Ronquist 1998, Liljeblad *et al.* 2008; Rokas *et al.* 2003, Ronquist and Liljeblad 2001, Ronquist and Nieves-Aldrey 2001, Stone and Cook 1998). The macrocynipoids form a basal paraphyletic grade falling into three lineages, the Austrocynipidae, Ibalidae, and Liopteridae. The microcynipoids (Cynipidae and Figitidae) are monophyletic and form two monophyletic sister lineages, the phytophagous Cynipidae and the parasitic Figitidae (*s. lato*) (Fig. 10).

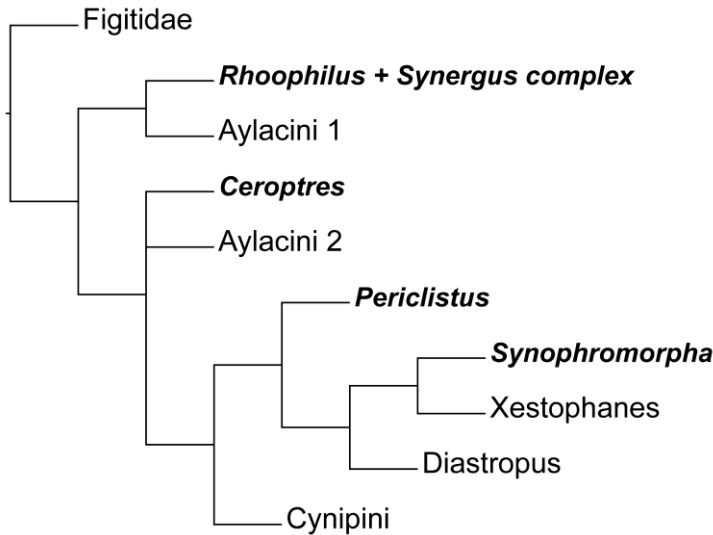


Figure 10. Relationships among Synergini (in bold) and other gall-inducing Cynipidae taxa (modified from Nylander 2004a)

The higher phylogeny of the Cynipidae was treated in several recent papers (Ronquist 1994, 1999, Liljeblad and Ronquist 1998, Liljeblad *et al.* 2008, Ronquist and Liljeblad 2001, Nylander 2004a). The phytophagous cynipid gall inducers and inquilines are forming a natural group. In addition to their unique phytophagous habit, a number of synapomorphies in their morphology is known (Liljeblad and Ronquist 1998). Liljeblad and Ronquist (1998), Ronquist (1994, 1999), Ronquist and Liljeblad (2001) divided Cynipidae into three groups: (i) inquilines (the tribe Synergini), (ii) the herb gallers (tribe Aylacini), and (iii) the woody rosid gallers (tribes Diplolepidini, Eschatocerini, Pediaspidini and Cynipini). A recent molecular phylogenetic analysis arised a conflict concerns the monophyly of the woody-rosid gallers, which all induce galls on woody members of the rosid clade of eudicots (Nylander 2004a). Based on DNA sequences, the woody-rosid gallers that are not associated with oaks (Diplolepidini, Eschatocerini and Pediaspidini) do not form a monophyletic group and are distantly related to Cynipini.

The Cynipidae comprise of 7 gall-inducing tribes and one inquilines tribe, Synergini. Early taxonomists (Hartig 1840, Ashmead 1903), based on morphological similarities, grouped all inquilines together. Others have suggested that the inquilines are polyphyletic, with each inquiline being more closely related to its particular gallwasp host (Askew 1984). Shorthouse (1980) thought that inquilines represent forms that never evolved the gall inducing capability on their

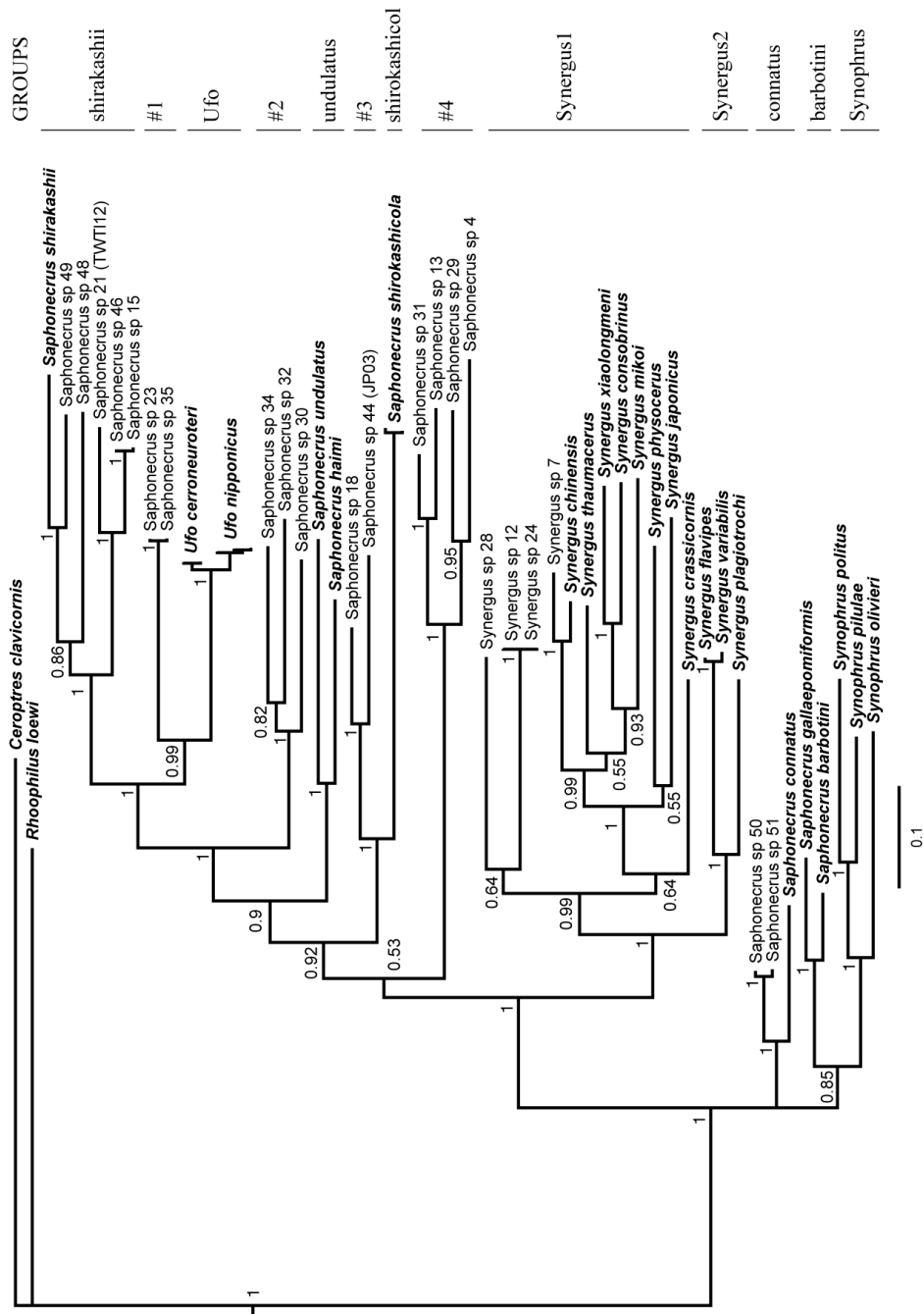


own. Morphological evidence has long supported the view that the Synergini are a monophyletic group that diverged from within a paraphyletic tribe (Aylacini) of herb gallwasps, with ancestry closest to the herb-galling genera *Diastrophus* and *Xestophanes* (Ronquist 1994, Ronquist and Liljeblad 2001, Liljeblad 2002, Liljeblad *et al.* 2008). Liljeblad (2002) hypothesized that cynipid inquilines in oak galls are derived from gall inducing cynipids close to *Diastrophus*, via an intermediate evolution of inquilinism in rose cynipid galls. This hypothesis placed the oak cynipid inquilines close to the rose cynipid inquilines, represented by species of *Periclistus* and *Synophromorpha* genera.

The inquilines are now believed to represent polyphyletic (or paraphyletic) assemblage, in which species associated with rose cynipids are distinct from those associated with oaks. Molecular phylogenetic evidence suggests that the inquilines are not a monophyletic group, and instead comprise up to 3 distinct evolutionary lineages with independent origins within the Aylacini assemblage: (i) rose-associates inquilines in *Synophromorpha* and *Periclistus*, (ii) oak-associated inquilines in *Ceroptres*, (iii) oak-associated inquilines in *Synophrus-Saphonecrus-Synergus-Ufo* and the Afrotropical genus *Rhoophilus* attacking moth-induced galls (Fig. 10) (Nylander 2004a, Melika 2006, van Noort *et al.* 2007, Liljeblad *et al.* 2008). However, the contradiction related to the origin of inquilines can not be considered as fully resolved. Phylogeny based on a more detailed taxon sampling is required.

Oak associated inquilines in *Ceroptres* form a distinct lineage, with independent origin, however, only western palaeartic species were involved into all molecular and morphological analyses. Morphologically *Ceroptres* species are quite distinct from all species within the Synergus complex. However, North American species resemble other inquilines more closely and some of them show apomorphic similarities with *Synergus* in the structure of the petiolar annulus (Ritchie 1984, Liljeblad and Ronquist 1998). Thus, it is possible that inclusion of the nearctic *Ceroptres* species might affect the conclusions reached earlier on inquilines relationships.

*Rhoophilus loewi* is the sister group of a lineage leading to a group of four genera of inquiline cynipids (*Saphonecrus*, *Synergus*, *Synophrus* and *Ufo*) attacking oak galls. This pattern allows two alternative hypotheses for the evolution of this oak cynipid lineage. One is that *Rhoophilus* is the sole known survivor of a once more diverse basal lineage of inquilines attacking a taxonomic diversity of host gall inducers on plants other than oaks. For some reason the oak cynipid inquilines represent a particularly successful descendant lineage of this group. The alternative is that *Rhoophilus* itself represents a southern African offshoot of an ancestral lineage otherwise closer in ecology and host plant association to the extant oak cynipid inquilines (van Noort *et al.* 2007).



GROUPS

shirakashii

#1

Ufo

#2

undulatus

#3

shirokashicol

#4

Synergus1

Synergus2

connatus

barbotini

Synophrus

Figure 11. (on the left) Preliminary phylogenetic tree of the *Synergus* complex. Known species are shown in bold in the tree and the newly established lineages are numbered. Group column assigns names to the lineages referred in the main text. The tree is based on a Bayesian reconstruction from a segment of 28S D2 and cytochrome oxidase I (*coxI*) gene sequences using MrBayes 3.1.2 parallel version (Ronquist and Huelsenbeck 2003). *Ceroptres* was set as the outgroup for rooting the tree. Posterior probabilities of clades are shown at the nodes. For wasp rearing, DNA laboratory protocol and sequencing we used the same methods as in Péntzes *et al.* (2009), except that a shorter, 636 bp fragment was used from the *coxI* gene. Sequences were aligned using Muscle 3.6 (Edgar 2004), with the default settings. Separate data partitions were defined for 28S D2 and the different *coxI* codon positions. According to MrModeltest 2.3 (Nylander 2004b), GTR+I+G substitution model was chosen for 28S D2 and 2<sup>nd</sup> codon positions of *coxI*, while GTR+G for the others. During the reconstruction, all four partitions were “unlinked” and rate parameter was set to variable. All other priors and MCMC settings were kept at their default value. Out of the 15 million generations of Markov chains, the first 8 million were dropped (burn-in). Convergence was acceptable according to the visual inspection, small average standard deviation of split frequencies and PSRF values. Details will be published elsewhere.

*Ufo* species are known only from the Eastern Palaearctic and the Oriental Region, synapomorphies and generic diagnostic characters of which were discussed in details (Melika *et al.* 2005, 2007, 2012). *Ufo* shares some morphological characters with two allied genera, *Saphonecrus* and *Synergus*. *Ufo* and *Saphonecrus*, have the radial cell along the forewing margin opened and the female antenna is 13-segmented; both *Ufo* and *Synergus* have a distinct pronotal carina but in *Synergus* the forewing is with a closed radial cell and the female antenna is 14-segmented (Melika *et al.* 2005). These shared morphological characters place *Ufo* into the *Synergus* complex of inquiline genera, phylogenetic analysis of which was recently published without *Ufo* and thus the phylogenetic position of which was still uncertain (Ács *et al.* 2010).

The recent phylogenetic reconstructions within the *Synergus* complex of species support the monophyly of the large genus *Synergus* and the smaller *Synophrus*, while the monophyly of *Saphonecrus* was rejected (Péntzes *et al.* 2009, Ács *et al.* 2010). These results are also supported by the new molecular phylogeny which we propose for the first time in this review (Table 9, Fig. 11).

Three main clades can be established, although their relationships are unresolved: “*Synophrus*+*barbotini*”, “*connatus*” and all others. The latter can be divided into two (or three as discussed below) lineages. One of them is the genus *Synergus*.

Table 9. Source of data in the phylogenetic reconstruction.

<b>Lineage</b>	<b>GenBank Accession number; D2, <i>coxI</i> (source)</b>
<i>Ceroptres clavicornis</i>	EF487120, EF486871 (Ács et al 2010)
<i>Rhoophilus loewi</i>	EF487123, EF486876 (Ács et al 2010)
<i>Saphonecrus barbotini</i>	EF487124, EF486877 (Ács et al 2010)
<i>Saphonecrus connatus</i>	EF487125, EF486878 (Ács et al 2010)
<i>Saphonecrus haimi</i>	EF487126, EF486879 (Ács et al 2010)
<i>Saphonecrus lusitanicus</i>	EF487131, EF486881 (Ács et al 2010)
<i>Saphonecrus shirakashii</i>	JX468370, JX468365 (Melika et al 2012)
<i>Saphonecrus shirokashicola</i>	JX468368, JX468362-63 (Melika et al 2012)
<i>Saphonecrus sp 13</i>	Unpublished
<i>Saphonecrus sp 15</i>	Unpublished
<i>Saphonecrus sp 18</i>	Unpublished
<i>Saphonecrus sp 23</i>	Unpublished
<i>Saphonecrus sp 32</i>	Unpublished
<i>Saphonecrus sp 35</i>	Unpublished
<i>Saphonecrus sp 4</i>	Unpublished
<i>Saphonecrus sp 46</i>	Unpublished
<i>Saphonecrus sp 48</i>	Unpublished
<i>Saphonecrus sp 50</i>	Unpublished
<i>Saphonecrus sp 51</i>	Unpublished
<i>Saphonecrus undulatus</i>	EF487133, EF486883 (Ács et al 2010)
<i>Saphonecrus_sp 21 (TWT112)</i>	JX468369, JX468364 (Melika et al 2012)
<i>Saphonecrus_sp 44 (JP03)</i>	JX468371, JX468366 (Melika et al 2012)
<i>Saphonecrus_sp_29</i>	Unpublished
<i>Saphonecrus_sp_30</i>	Unpublished
<i>Saphonecrus_sp_31</i>	Unpublished
<i>Saphonecrus_sp_34</i>	Unpublished
<i>Saphonecrus_sp_49</i>	Unpublished
<i>Synergus chinensis</i>	EF487140, EF486890 (Ács et al 2010)
<i>Synergus consobrinus</i>	EF487189, EF486954 (Ács et al 2010)
<i>Synergus crassicornis</i>	EF487147, EF486898 (Ács et al 2010)
<i>Synergus flavipes</i>	EF487151, EF486903 (Ács et al 2010)
<i>Synergus japonicus</i>	EF487167, EF486927 (Ács et al 2010)
<i>Synergus mikoi</i>	EF487169, EF486928 (Ács et al 2010)
<i>Synergus physocerus</i>	EF487185, EF486950 (Ács et al 2010)
<i>Synergus plagiostrochi</i>	EF487187, EF486952 (Ács et al 2010)
<i>Synergus sp 12</i>	Unpublished
<i>Synergus sp 24</i>	Unpublished

<i>Synergus sp 24B</i>	Unpublished
<i>Synergus sp 28</i>	Unpublished
<i>Synergus sp 7</i>	Unpublished
<i>Synergus thaumacerus</i>	EF487191, EF486956 (Ács et al 2010)
<i>Synergus variabilis</i>	EF487219, EF486967 (Ács et al 2010)
<i>Synergus xiaolongmeni</i>	EF487220, EF486968 (Ács et al 2010)
<i>Synophrus olivieri</i>	EF583959, EF579725 (Pénzes et al 2009, Ács et al 2010)
<i>Synophrus pilulae</i>	EF487224, EF579725 (Pénzes et al 2009, Ács et al 2010)
<i>Synophrus politus</i>	EF487223, EF579710 (Pénzes et al 2009, Ács et al 2010)
<i>Ufo cerroneuroteri</i>	JX468367, JX468357-58 (Melika et al 2012)
<i>Ufo nipponicus</i>	JX468367, JX468359-61 (Melika et al 2012)

However, what concern the monophyly of *Synergus*, it is important to state that only western and eastern palaeartic *Synergus* species were involved into these analyses, so the monophyly of worldwide *Synergus* must be treated carefully. Many species assigned to the nearctic *Synergus* morphologically strongly differs from palaeartic ones. Preliminary unpublished analysis showed at least three distinct morphological groups within the nearctic *Synergus* and thus involving those into phylogenetic analyses might strongly change our current interpretation of the genus. Ács *et al.* (2010) showed that the palaeartic *Synergus* is a monophyletic group, and the Eastern Palaeartic *S. chinensis*, *S. xiaolongmeni* and *S. japonicus* nested among the Western Palaeartic species and thus, there is no evidence that the Eastern and Western Palaeartic *Synergus* species represent discrete radiations. Ács *et al.* (2010) also showed that Mayr's long-accepted morphology-based sections I and II within the genus *Synergus* do not represent natural groups, and should be abandoned. For example, the widely-used Folmer barcode region of the mitochondrial *coxI* gene has excellent potential to define "molecular taxa" (MOTU) in the *Synergus* complex: some recognised *Synergus* species corresponded to MOTUs others clearly do not (Ács *et al.* 2010). There is one split within *Synergus* ("Synergus 1" and "Synergus 2", Figs. 11, 17). "Synergus 2" group includes 3 western palaeartic species, *S. flavipes*, *S. variabilis*, *S. plagiostrochi*, all known to associate with section Cerris oaks, while "Synergus 1" group includes those species, which prefer non-cerris section oaks. However, subclade "Synergus sp. 28, 12, 24" within "Synergus 1" includes undescribed eastern palaeartic species which from "Synergus sp 12, 24" associate with section Cerris, while "Synergus sp 28" with section Quercus oaks. Three species in the "Synergus 2" subclade bear two morphological peculiarities: the absence of lateral pronotal and lateral frontal carinae while species in "Synergus 1" subclade have strong lateral pronotal and frontal carinae except *S.*

*consobrinus* which lack these two characters. Thus, the two subclades within *Synergus* hard to tell apart based on their morphology.

*Synophrus* with the 7 known western palaeartic species forms a monophyletic group, morphologically similar to *Saphonecrus* in the absence of the lateral frontal carinae, opened radial cell in the forewing, but the lateral pronotal carina is absent, the pronotum is rounded in dorsal view and the male antennae has 13 flagellomeres; while in *Saphonecrus* the lateral pronotal carina present, the pronotum with sharp angles in dorsal view and the male antennae has 12 flagellomeres. Phylogeny of *Synophrus* has been recently evaluated in details (Pérez *et al.* 2009).

Earlier data had been supported the hypothesis that all *Synophrus* species, together with *Saphonecrus gallaepomiformis* and *S. barbotini*, form a monophyletic group (Pérez *et al.* 2009, Ács *et al.* 2010). Neither molecular nor morphological data support the maintenance of *Saphonecrus* as a monophyletic group, and hence it cannot be diagnosed as a distinct genus. The main features that can be used to associate the two above-mentioned *Saphonecrus* species with *Synophrus* are (i) the absence of the lateral pronotal carina, the pronotum is rounded in dorsal view and (ii) the male antennae with 13 flagellomeres. This indicates that *Saphonecrus barbotini* and *S. gallaepomiformis*, should be transferred to *Synophrus*. However, some peculiarities of their biology, distribution, host gallwasp and host plant associations as well as morphological differences (shape of the head and metasoma, the sculpture of the mesoscutum, completeness of notauli, Figs. 4, 7) suggest that they might be well treated as separate genera (nomenclatorial changes will be done elsewhere).

The placement of *Saphonecrus connatus*, the type species of *Saphonecrus*, is crucial to decide the status of *Saphonecrus*. The “connatus” clade with *S. connatus* (Fig. 5) and two other Eastern Palaeartic lineages (sp 50 and sp 51 from Russia and Japan, respectively, Fig. 11), shares the two above mentioned synapomorphies of *Saphonecrus barbotini*, *S. gallaepomiformis* and *Synophrus* spp. The molecular evidence is equivocal with regard to the position of *S. connatus* and allied species. All the molecular data together with some morphological peculiarities, suggests that it is clearly a distinct unit (genus), different from the “barbotini” clade. It is a separate early lineage within the complex of species.

The third clade of eastern *Saphonecrus*, the “undulatus” group, known also earlier (Pérez *et al.* 2009, Ács *et al.* 2010) is very distant from “barbotini” and “connatus” clades and not only by molecular evidences but also morphologically they possess a number of synapomorphies: the shape of the head and its sculpturing, the presence of a strong lateral propodeal carina, the absence of notauli, very short mesoscutum and others (Fig. 3). Consistently with the molecular phylogeny (posteriori probability 1, Fig. 11), all other clades of *Saphonecrus*, including the *Ufo* genus, bear the same morphological peculiarities

as the “undulatus” group and thus differs from the “connatus” and “barbotini” groups and *Synophrus*.

The “shirakashii” clade is a sister clade to “saphonecrus #1”+*Ufo*. In “shirakashii” lineages the mesoscutum is always with short irregular transverse striae and the surface between them is shiny, smooth; the head is quadrangular in front view, more robust; the metasoma of females more elongated (Fig. 12) while in “saphonecrus #1” the mesoscutum is delicately alutaceous or punctuate, without distinct short irregular transverse striae; the head is ovate and less robust from above, the female metasoma is more rounded (Fig. 13). The *Ufo* species strictly associate with section Cerris oaks only and their morphology is also very peculiar (Fig. 8), synapomorphies and genetic distances of *Ufo* from the “shirakashii” group were discussed in details in Melika *et al.* (2012). All species of the “shirakashii” and “saphonecrus #1” are known to associate exclusively with the *Quercus* subgenus *Cyclobalanopsis* (see the chapter on host plant associations below).

“Saphonecrus #2”, the sister group of “shirakashii” + “saphonecrus #1” + *Ufo*, is known to associate with *Lithocarpus* and *Cyclobalanopsis*. In the females of “saphonecrus #2” species the lower face and malar space is uniformly striate, with striae reaching antennal toruli; the height of eye is 1.9 times as high as the length of the malar space; the occiput and gena are smooth, shiny; antennal pedicel 1.7 times as long as broad; the mesoscutum+mesoscutellum as long as height of the mesosoma; scutellar foveae with smooth, shiny bottom while in “saphonecrus #1” species the malar space with striae, the lower face only laterally striate, with indistinct striae do not reaching antennal toruli, the mid part of the lower face without striae; the occiput and gena are uniformly alutaceous; the height of the compound eye 1.7 times as high as length of the malar space; antennal pedicel 2.5 times as long as broad; the mesoscutum+mesoscutellum 1.2 times as long as height of the mesosoma; scutellar foveae with smooth, shiny bottom, with few wrinkles (Fig. 14).

Morphological peculiarities of “shirokashicola” (Fig. 15) and “saphonecrus group #3”, both associated with *Cyclobalanopsis*, are given in details in Melika *et al.* (2012).

Morphologically a very distinct group is “saphonecrus #4”, species of which exclusively associated with *Lithocarpus*, and possess a number of unique morphological features in between all known *Saphonecrus* clades: rounded robust head with strong frontal carinae, strong wrinkles in scutellar foveae and the metasoma of which is punctuated (Fig. 16). Note also that its phylogenetic position within the third main lineage is weakly supported (posteriori probability 0.53, Fig. 11).

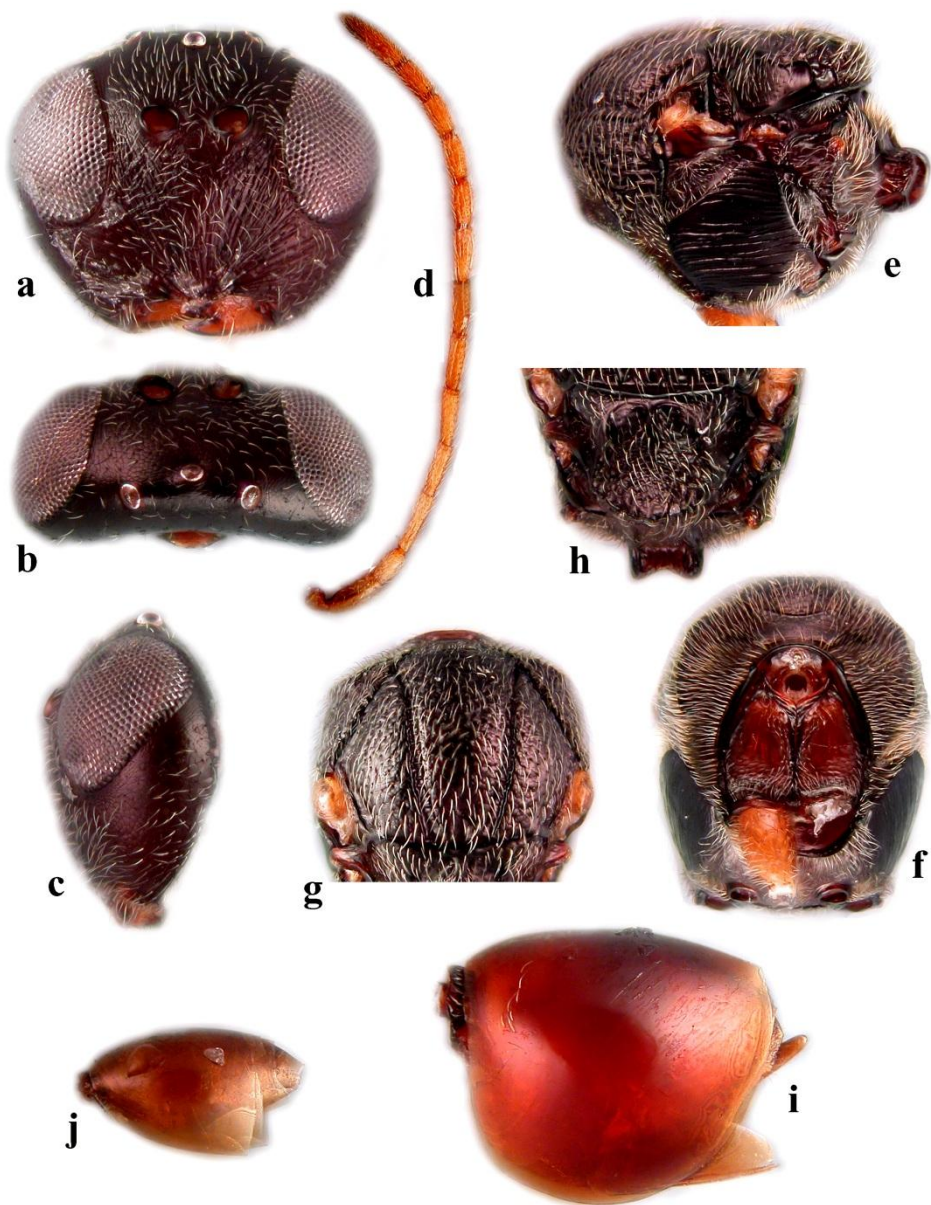


Figure 12. *Saphonecrus shirakashii* (shirakashii group): a–g, female: a, head, anterior view, b, head, dorsal view, c, head, lateral view, d, antenna, e, mesosoma, lateral view, f, mesosoma and propleura, anterior view, g, pronotum and mesoscutum, dorsal view, h, mesoscutellum, dorsal view, i, metasoma, lateral view, j, metasoma, lateral view, male.



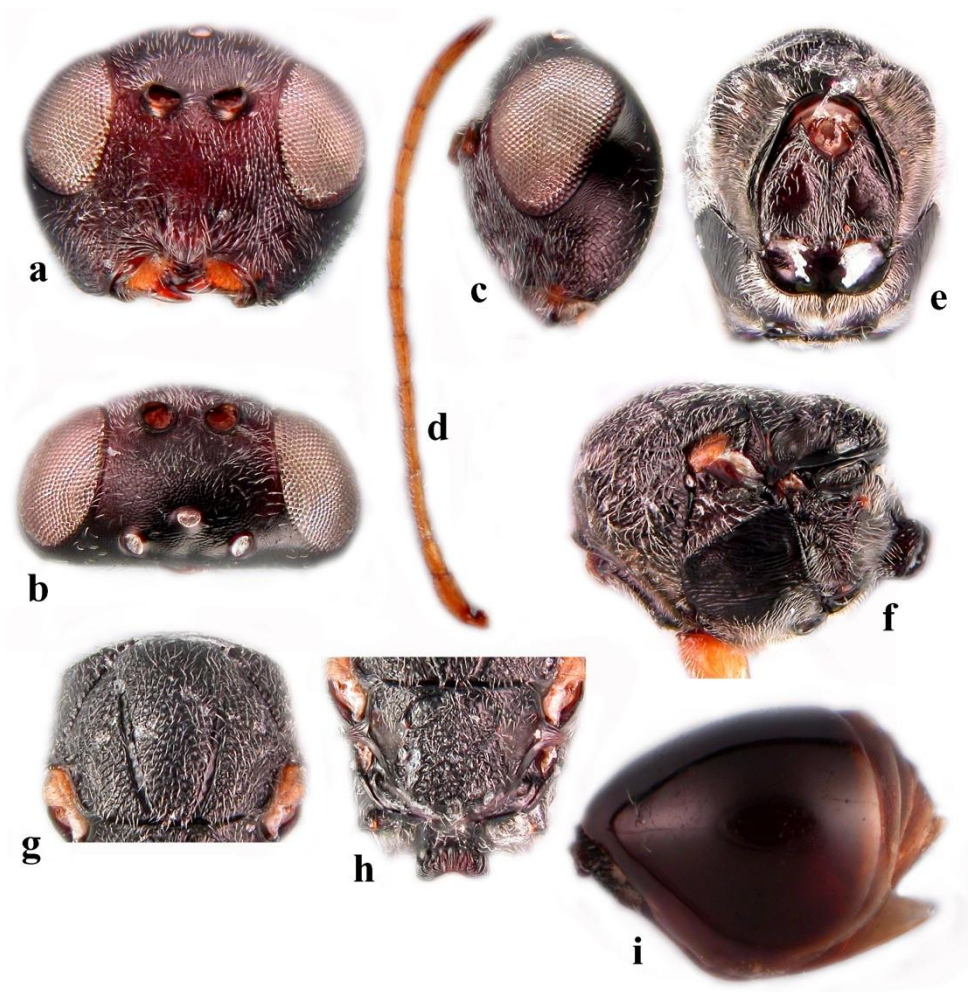


Figure 13. *Saphonecrus* “sp23, sp35” (*saphonecrus* group #1, Fig. 11), female: a, head, anterior view, b, head, dorsal view, c, head, lateral view, d, antenna, e, mesosoma and propleura, anterior view, f, mesosoma, lateral view, g, pronotum and mesoscutum, dorsal view, h, mesoscutellum, dorsal view, i, metasoma, lateral view.

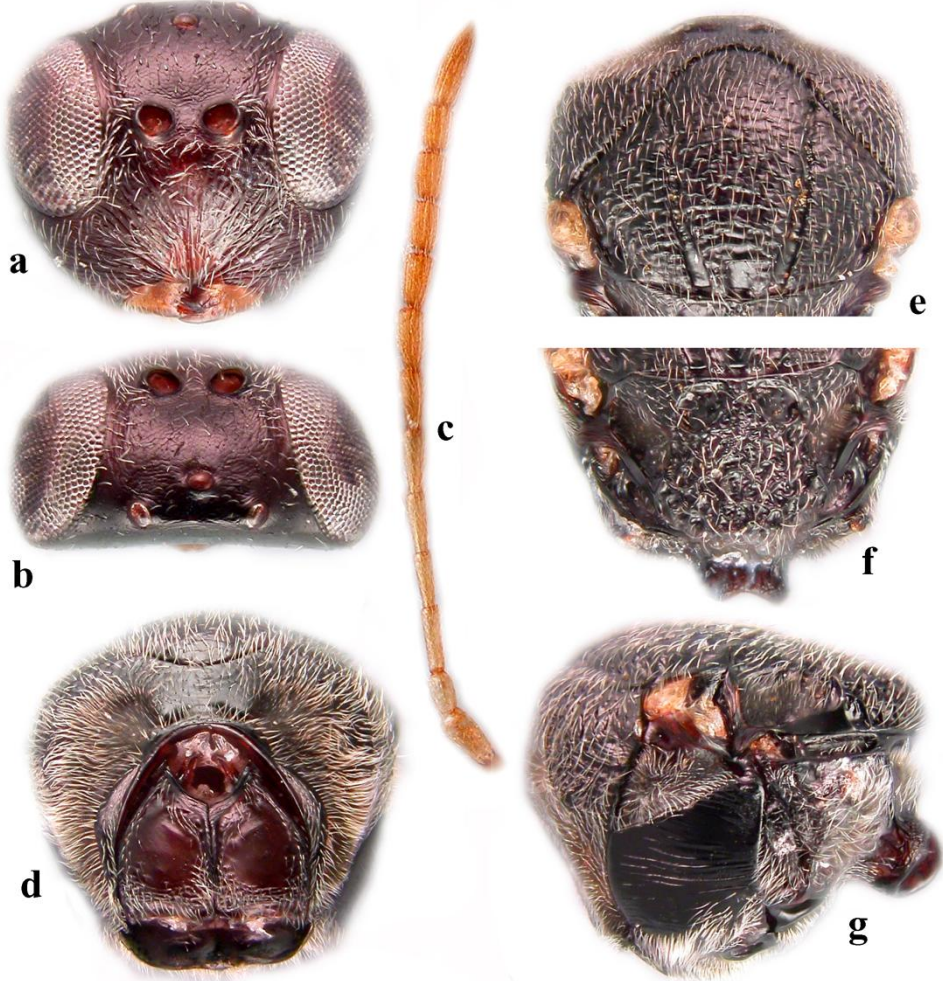


Figure 14. *Saphonecrus* “sp30, 32, 34” (*saphonecrus* group #2, Fig. 11), female: a, head, anterior view, b, head, dorsal view, c, antenna, d, mesosoma and propleura, anterior view, e, pronotum and mesoscutum, dorsal view, f, mesoscutellum, dorsal view, g, mesosoma, lateral view.

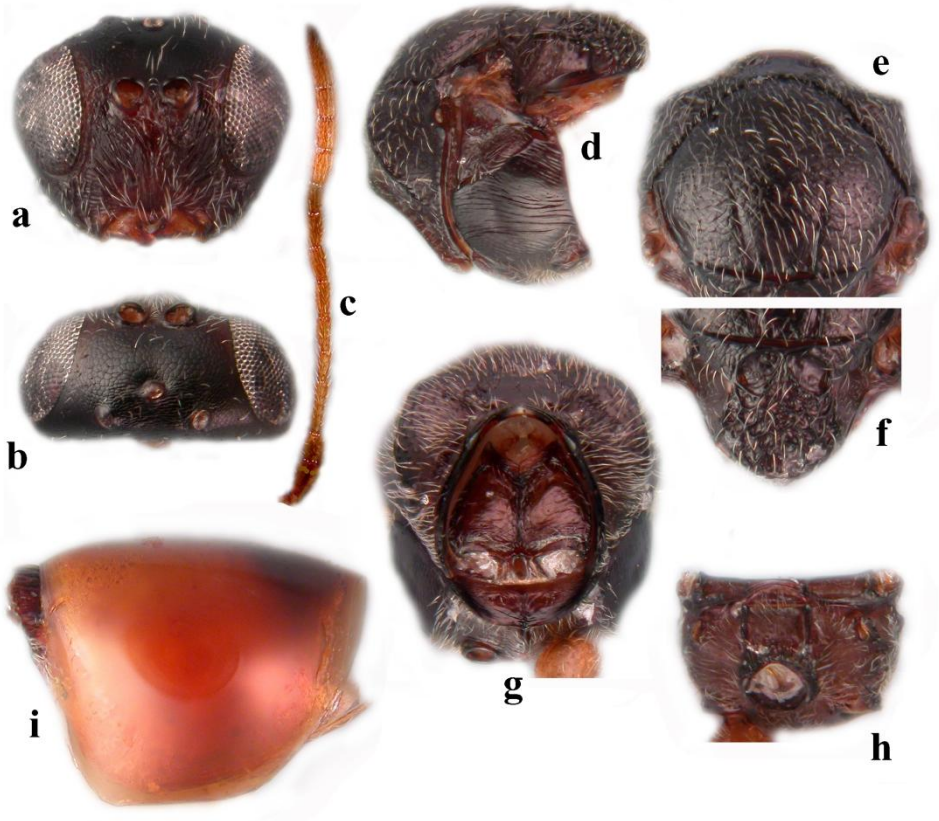


Figure 15. *Saphonecrus shirokashicola* (shirokashicola group, Fig. 11), female: a, head, anterior view, b, head, dorsal view, c, antenna, d, mesosoma, part, lateral view, e, pronotum and mesoscutum, dorsal view, f, mesoscutellum, dorsal view, g, mesosoma and propleura, anterior view, h, metascutellum and propodeum, anterodorsal view.

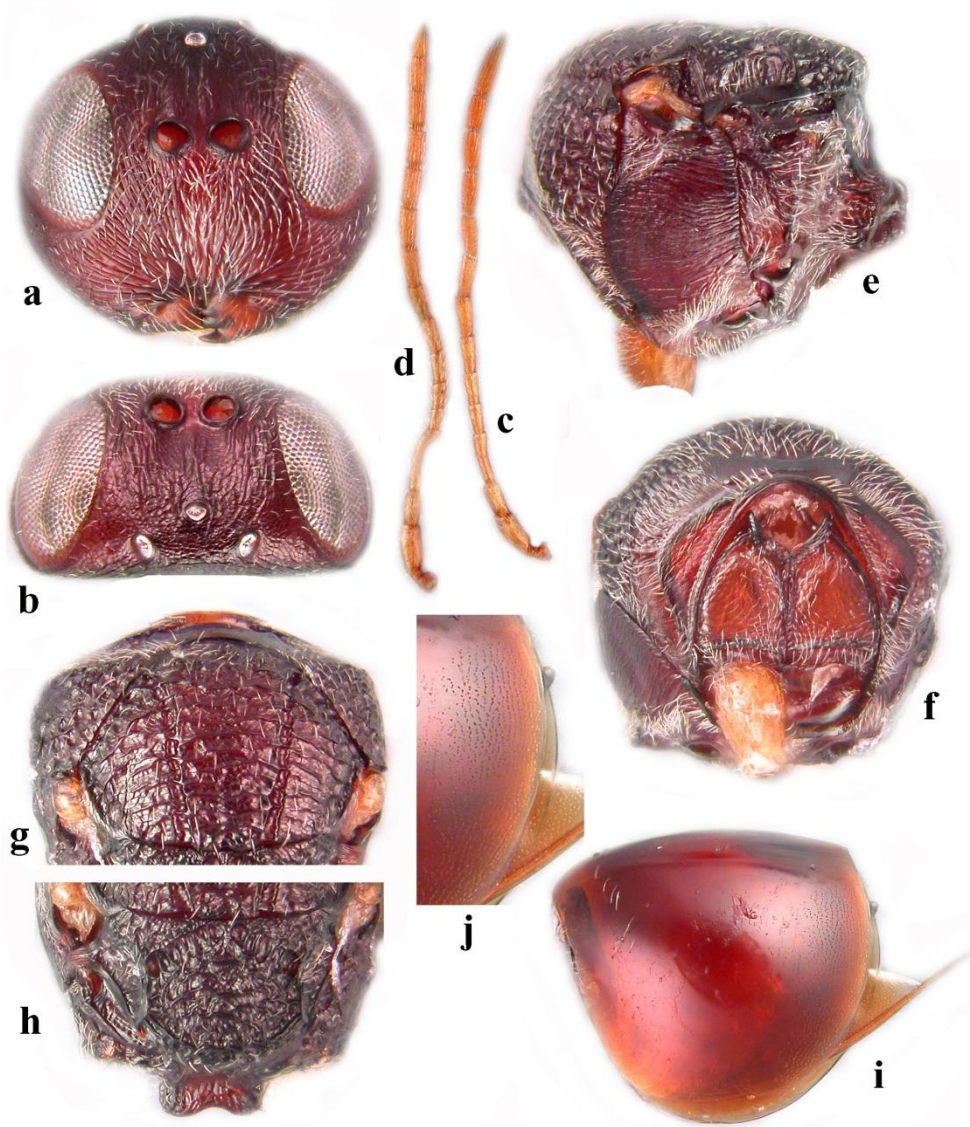


Figure 16. *Saphonecрус* “sp31, 13, 29, 4” (*saphonecрус* group #4, Fig. 11): a–b, female: a, head, anterior view, b, head, dorsal view. c–d, antenna: c, female, d, male. e–j, female: e, mesosoma, lateral view, f, mesosoma and propleura, anterior view, g, pronotum and mesoscutum, dorsal view, h, mesoscutellum, dorsal view, i, metasoma, lateral view, j, metasoma, part, lateral view.

No doubts, that the current limits of the *Saphonecrus* genus must be changed, a number of new monophyletic genera must be established. Nomenclatorial changes with the erection of new genera and detailed morphological diagnoses, with the description of new species from the Eastern Palaearctic and the Oriental Region (Taiwan) will be done elsewhere. Also the two known *Saphonecrus* species from Phillipines as well as some of the nearctic *Saphonecrus* species must be treated in separate genera.

## Host gall associations of oak cynipid inquilines

The world catalogue of cynipid inquilines with host gallwasp and host plant associations is quite old (Dalla Torre and Kieffer 1910); the most recent comprehensive study can be found in Ritchie (1984). The oak gallwasp associations of the Western Palaearctic oak inquilines, *Ceroptres*, *Saphonecrus*, *Synergus* and *Synophrus*, were under research prolong centuries and a huge literature concerning the gall-inducer – inquilines relations is available (e.g., Hartig 1840, 1843, Mayr 1872, Eady and Quinlan 1963, Nieves-Aldrey and Pujade-Villar 1985, 1986, Pujade-Villar 1992, Pujade-Villar and Nieves-Aldrey 1990, 1993, Nieves-Aldrey 2001, Pujade-Villar *et al.* 2003, Melika 2006 and many others). Recently all available host association data on the Western Palaearctic inquilines was collected in one review (Askew *et al.* 2012, *in press*), except those species described from Iran (Sadeghi *et al.* 2006). Last review for the Eastern Palaearctic was made by Abe *et al.* (2007). Rather less has been published on the Nearctic fauna and all relevant earlier published data were collected in Weld (1952) and Burks (1979). The Neotropical (Ritchie and Shorthouse 1987a, Nieves-Aldrey 2005, Nieves-Aldrey and Medianero 2010, 2011) and Oriental (Abe *et al.* 2007, Wang *et al.* 2010, Liu *et al.* 2012, Melika *et al.* 2012) Regions are the most poorly studied, fragmentary data only available.

The host associations of non-oak cynipid inquilines, *Periclistus*, *Rhoophilus*, *Synophromorpha*, were briefly introduced earlier. Here we deal only with those genera which are associated with gallwasps on oaks and near oak genera: *Ceroptres* and the *Synergus* complex (*Agastoroxenia*, *Saphonecrus*, *Synergus*, *Synophrus* and *Ufo*). Most oak cynipid inquiline species tracking the distributions of their host galls, which in turn track the ranges of their host oak species. The inquilines with the most extensive geographic ranges are generalists associated with widely distributed oaks. The most extreme example is *Synergus facialis*, which attacks 53 different oak cynipid hosts (Askew *et al.* 2012, *in press*). Data to date show some oak inquiline species to have restricted, regional ranges. For example, *Synergus plagiotrochi*, *S. ibericus*, *S. ilicinus*, *Synophrus olivieri*, *S. pilulae*, *Saphonecrus gallaepomiformis* and *S. undulatus* tend to attack only a narrow range of host galls, and are often associated with *Quercus* species that

themselves have relatively limited geographical distributions (e.g. *Quercus cerris*, *Q. ilex*, *Q. suber*, *Q. coccifera*, *Q. faginea* in Europe). *Synergus ibericus* and *S. ilicinus* are only known from Spain and France, *Synergus subterraneus* only from Spain, *S. consobrinus* only from Austria and Hungary, and *S. diaphanus* from the Balkans eastwards towards Iran (Pujade-Villar *et al.* 2003). These patterns suggest that, as for gall-inducers, inquiline cynipids show region specific faunas that coincide with long-established glacial refuges in southern Europe (Stone *et al.* 2001, Rokas *et al.* 2003) as shown recently for a generalist species, *Synergus umbraculus* (Bihari *et al.* 2011). Based on the essential knowledge of the oak cynipid inquilines of the Western Palaearctic, they can be classified into three general categories.

One group of species are virtually host-specific, having been recorded from only a single host, e.g. *Synergus diaphanus*, *S. physocerus*, *S. subterraneus*, *Synophrus* species, some *Saphonecrus* species. The proportion of species in this category contrasts with other zoogeographical regions, where majority of cynipid inquiline species are known only from a single host gall (Burks 1979 for the Nearctic; Abe *et al.* 2007 for the Eastern Palaearctic; Ritchie and Shorthouse 1987a, Nieves-Aldrey 2005, Nieves-Aldrey and Medianero 2010, 2011 for the Neotropics). However, cynipid inquilines from other zoogeographical regions are far less studied than the Western Palaearctic fauna, and many personal records show that the apparent specificity in those regions is an artefact of limited sampling (GM unpubl. data). In other cases, notably for *Synophrus*, it is hard to establish host diversity (discussed above).

A second group of species (e.g. *Ceroptres cerri*, *Saphonecrus gallaepomiformis* and *Synergus hayneanus*) show moderate host ranges for the group, and are associated with up to 20 different host galls. The host galls generally share some biological characteristics, such as the host gall shape, the host oak taxon or the host plant organ on which the host gall is induced. This fact suggests “entry points” for inquilines, but this topic is not yet explored.

The third group contains those inquilines known to attack more than 20 different host galls (e.g. *Ceroptres clavicornis*, *Synergus pallicornis*, *S. pallipes* and *S. umbraculus*). The European inquiline species recorded from the largest number of different galls is *S. facialis* with 53 different host galls, *S. umbraculus* is one of the commonest oak cynipid inquilines in the Western Palaearctic, and attacks more than 30 different oak gall hosts (Pujade-Villar *et al.* 2003, Askew *et al.* 2012, *in press*).

Inquiline host specificity can also be considered in terms of the inquiline richness associated with specific galls. The majority of gallwasp species are attacked by 1 or 2 inquiline species, around 50% of known Western Palaearctic species support 2–5 inquiline species while only ca. 10% support more than 5 inquilines species. The most extensively studied European oak galls for which the most inquiline species have been recorded are those of the asexual generation of

*Andricus kollari* complex (14 species), *A. lignicolus*, *A. quercustozae*, *A. quercuscalicis* and *A. coriarius*, and the sexual generation galls of *Andricus curvator* and *Neuroterus quercusbaccarum*. Of course, that in interpreting host ranges, we must take into account that the well-studied taxa are much better sampled than those of less studied gall species and thus the records are highly biased (Sanver and Hawkins 2000).

Little is known about the factors determining inquiline host range in oak gall hosts. Phenological matching with the host gall – an appropriate developmental stage – must be crucial, particularly for lethal species that must attack the host larval chamber early in gall development. Host associations of such species are more likely to be defined by phenological “windows of opportunity”. No doubts, that the developing of special morphological structures (hairs, spines, surface coatings of sticky resins), increases in gall wall thickness, that have been interpreted as gall defences, probably enhance protection of the gall inducer against lethal inquilines and parasitoids (Stone and Cook 1998, Stone and Schönrogge 2003, Bailey *et al.* 2009, Stone *et al.* 2012). The significance of resource availability is illustrated by the fact that the small pip-like bud and catkin sexual generation galls of many *Andricus* species have few or no inquilines (Stone *et al.* 1995).

Majority of inquiline species are associated with species within a single host genus while some of them are present in galls of five or even more host genera. The number of inquiline species associated with each host cynipid genus increases with the number of host gall forms per genus (Melika 2006). There is a weaker positive correlation between the number of host specific inquiline species and the total number of inquiline species associated with each host cynipid genus. Exceptions to this trend are the genera *Plagiotrochus* with more host-specific inquiline species than expected, and *Neuroterus* with fewer host-specific inquiline species. It is not clear yet what the selective benefits of specialisation for inquilines are. Are they better synchronised with their host galls, or, compared to generalists, more competent to manipulate the tissues in their host galls?

Similarities in the inquiline faunas associated with different host genera might be explained by other factors, namely history. In the Western Palaearctic, for example, two main generic groupings are apparent: (i) one group includes *Plagiotrochus*, *Chilaspis*, *Dryocosmus* and *Aphelonyx*, while the second includes the remaining genera, including *Andricus*. The phylogenetic relationships among genera of oak cynipid gallwasps suggest that closely related gall inducers share inquilines recruited by their common ancestors (Ronquist 1994, 1995, 1999, Liljeblad and Ronquist 1998, Ronquist and Liljeblad 2001, Liljeblad *et al.* 2008, Stone *et al.* 2009, Ács *et al.* 2010).

It is also possible that the groupings reflect similarities in traits used by inquilines to select hosts, regardless of gallwasp and inquiline relatedness. *Aphelonyx*, *Chilaspis*, *Dryocosmus*, *Plagiotrochus* and some other genera are

associated entirely or predominantly with oak hosts in the oak section *Cerris* while others associate with other *Quercus* section and oak related genera. The host plant associations of inquilines are considered further below.

Further we shall discuss in details the host gallwasp associations within different oak cynipid inquiline genera.

***Ceroptres*.** Two western palaeartic *Ceroptres* species are known only. *Ceroptres clavicornis* is a generalist, has been reared from 30 different cynipid host galls, on section *Quercus* oaks (white oaks) (Askew *et al.* 2012, *in press*). No preferred gallwasp genus was found for this species, it was reared mainly from galls of *Andricus* (usually asexual forms), but also associates with *Callirhytis*, *Cynips* and *Neuroterus* (Pujade *et al.* 2003). *Ceroptres cerri* appears to be more specialised and attacks galls of a some sexual forms of *Andricus* species, *Aphelonyx cerricola* (Giraud), *Dryocosmus cerriphilus* (Giraud), *Cerroneuroterus* and *Plagiotrochus* species and was recorded also in galls affected by *Synophrus politus* (Pujade *et al.* 2003), all on section *Cerris* oaks (Pujade *et al.* 2003, Melika 2006).

Four eastern palaeartic *Ceroptres* species, *C. distinctus*, *C. kovalevi*, *C. masudai*, and *C. setosus* are known (Abe *et al.* 2007, Wang *et al.* 2012). *Ceroptres kovalevi* was reared from unidentified galls (Belizin 1973). *C. masudai* is known from galls of *Andricus kashiwaphilus*, *A. mukaigawae* and *Trigonaspis* (= *Ussuraspis*) *nervosa* (Kovalev) from Japan and Russia (Abe 1997, GM, personal data); from *A. targionii* in Japan (Abe 1997); from leaf galls of undescribed *Trigonaspis* (= *Ussuraspis*) sp. in Russia (GM, personal data); occasionally emerged from galls of *Callirhytis hakonensis* Ashmead (= *A. symbioticus* Kovalev) (Wachi and Abe 2009). Gall host associations of two species described from China are unknown (Wang *et al.* 2012).

Nearctic *Ceroptres* species are known to associate with 4 *Andricus* Hartig, 2 *Callirhytis* Förster, 1 *Bassettia* Ashmead, 1 *Acraspis* Mayr, 1 *Xanthoteras* Ashmead and 1 *Neuroterus* Hartig species (Burks 1979). One nearctic species, *C. montensis*, known from California only, was reared from the galls of *Andricus reniformis* McCracken et Egbert which associate with the *Protobalanus* section oaks (Weld 1952).

One nearctic species, *C. inermis*, is known to associate with a gall-midge, *Cincticornia pilullae* (Osten Sacken) (Diptera: Cecidomyiidae) (Burks 1979); another *Ceroptres* has been recorded from rose cynipid galls (Ritchie 1984), however, this record should be confirmed.

No species of *Ceroptres* are known yet from the Neotropics.

***Agastoroxenia*.** This genus, with only one known species, *Agastoroxenia panamensis* Nieves-Aldrey & Medianero, is distributed in Panama, an inquiline in



unidentified *Andricus* induced stem galls on *Q. lancifolia* (red oaks) (Nieves-Aldrey and Medianero 2010).

***Saphonecrus*.** Currently 23 species of *Saphonecrus* are known worldwide (Table 5). All known *Saphonecrus* species except two, are inquiline in oak and oak-related cynipid galls.

The western palaeartic species are associated mainly with galls induced on section Cerris oaks, including Mediterranean evergreen species (*Q. ilex*, *Q. suber*, *Q. coccifera*) and *Q. cerris* in Central Europe. Three species, *Saphonecrus haimi*, *S. irani* and *S. undulatus*, which form a monophyletic group and have one generation per year, attack galls of *Aphelonyx cerricola* (Giraud), *Cerroneuroterus lanuginosus* (Giraud), *Chilaspis nitida* (Giraud), *Ch. israeli* (Sternlicht), *Pseudoneuroterus saliens* (Kollar) and galls modified by *Synophrus politus* (Pujade-Villar *et al.* 2003, Melika 2006). Two species, *S. barbotini* and *S. gallaepomiformis*, which formed the second monophyletic lineage within *Saphonecrus* and associated with Mediterranean evergreen oak species (*Q. ilex*, *Q. suber*, *Q. coccifera*) and have two generations per year, attacks *Plagiotrochus* galls only, especially woody galls of *P. britaniae* Barbotin and *P. coriaceus* (Mayr) in twigs (Pujade-Villar and Nieves-Aldrey 1990). The third clade is formed by the western palaeartic *S. connatus* and two undescribed eastern palaeartic *Saphonecrus* species reared from galls on white oaks in the Far East of Russia and Japan (Hokkaido) (GM, personal data). *Saphonecrus connatus* attacks some *Andricus* species and galls of *Callirhytis glandium* (Giraud), *Cynips quercusfolii* (L.), *Neuroterus anthracinus* (Curtis) and *N. quercusbaccarum* (L.). Two undescribed *Saphonecrus* species from the Far East of Russia and Japan were reared from undescribed bud galls and the asexual galls of *Callirhytis hakonensis* (= *Andricus symbioticus*).

From 13 described Eastern Palaeartic and Oriental *Saphonecrus* species for 8 species no gallwasp and plant host associations are known (Table 5). *Saphonecrus excisus* was reared from *Neuroterus haasi* Kieffer galls (Dalla Torre and Kieffer 1910). Two species, *S. shirakashii* and *S. shirocashicola*, were reared from undescribed leaf galls which belong to the newly described *Cycloneuroterus* genus (Tang *et al.* 2012b). Number of new Taiwanese *Saphonecrus* species and new genera, related to *Saphonecrus*, which for the host gallwasp associations are known also, are under description and will be published elsewhere soon.

For three nearctic *Saphonecrus* species host gall associations are known: *S. brevis* was reared from galls of *Andricus ruginosus* Bassett, *S. favanus* (taxonomic position of which is problematic) – from root galls of *Dryocosmus favus* Beutenmüller (taxonomic assignment of which is problematic, Ács *et al.* 2007), *S. gemmariae* – from stem swelling-like galls of *Callirhytis quercusgemmariae* (Ashmead) (Burks 1979).

Two *Saphonecrus* species are known to associate with non-cynipid oak galls. *Saphonecrus haimi* may occasionally occur in cecidomyiid galls and was reared from *Janetia cerris* (Kollar) (Diptera: Cecidomyiidae) galls on *Q. cerris* leaves (Melika 2006). *Saphonecrus yukawai* described from Japan, known to associate with the gall midge *Ametrodiplosis acutissima* (Monzen) (Diptera: Cecidomyiidae) on Cerris section oak, *Q. acutissima* only (Wachi *et al.* 2011a). Because *S. yukawai* has been reared only from *A. acutissima* galls on *Q. acutissima*, this new inquiline is probably the first known species specialized to depend on cecidomyiid galls. Numerous cecidomyiid species are known to induce galls on *Fagus* sp., however, only a few species of this family are known to induce galls on *Quercus* sp. (Yukawa and Masuda 1996, Yukawa *et al.* 2005).

**Synergus.** Host gall associations of the western palaeartic *Synergus* species are well-known and were analysed in many works in details (Nieves-Aldrey 2001, Pujade *et al.* 2003, Melika 2006, Askew *et al.* 2012, *in press*) and already were presented above.

Data on the gallwasp associations of the nearctic *Synergus* is very poor and majority of records are only those given in the original description of species, all data on which was collected in Burks (1979). Only one species, *S. agrifoliae*, is known to associate with genus *Neuroterus*; one-one species with *Acraspis*, *Belonocnema*, *Xanthoterus*, 2 with *Atrusca*, 3 with *Amphibolips*, 3 with *Heteroecus*, 6 with *Andricus*, 11 with *Disholcaspis*, and 12 with *Callirhytis*. Usually only one species of *Synergus* is known for one-one gallwasp species, however, some of them support more, for example, *Heteroecus pacificus* (Ashmead) – 3 species, *Callirhytis quercuspomiformis* (Bassett) – 5 species (Burks 1979).

Gall associations of the neotropical species were also discussed (Ritchie and Shorthouse 1987a, Nieves-Aldrey 2005, Nieves-Aldrey and Medianero 2011).

From 10 Eastern Palaeartic *Synergus* species only for two species, the bivoltine *S. gifuensis* and univoltine *S. japonicus*, the host associations are known (Abe *et al.* 2007). The first generation of *Synergus gifuensis* develops in the asexual galls of *Andricus mukaigawae* and *A. kashiwaphilus* while the second emerges from sexual galls of *Biorhiza weldi*; *S. japonicus* associates with the asexual galls of *A. mukaigawae* and *A. kashiwaphilus* (Abe 1990, 1992, Pujade-Villar *et al.* 2002). One species, *S. itoensis*, appeared to have a capability to induce its own gall in the seed coat of the acorn of *Q. (C.) glauca* (Abe *et al.* 2011). Eight new *Synergus* species from Japan, Far East of Russia and Taiwan, which for the host gallwasp associations are known also, are under description and will be published elsewhere soon.

One western palaeartic species, *Synergus variabilis*, has been also reared from galls of the cecidomyiid gall midges *Janetia cerris* (Kollar) and *Dryomyia circinnans* Giraud (Diptera, Cecidomyiidae) (Askew 1999).

*Synophrus*. Pujade-Villar *et al.* (2003) observed that *Synophrus politus* emerged from irregularly spherical and highly lignified stem swelling galls that developed over the summer in the exact location in which spring bud galls of a known gall inducing wasp, *Andricus burgundus* Giraud, were initiated. This modification of the host gall is extreme among cynipid inquiline, and in contrast to some inquiline cynipids, attack by *Synophrus* is always lethal to the host gallwasp. The host of *Synophrus* is very small at the time of inquiline attack, and is crushed and disintegrates in the first stages of inquiline takeover. The resulting *Synophrus*-controlled gall morphologies are specific to particular *Synophrus* species, as is also the case in true gall inducers. Other gallwasp hosts may be usurped in this way, but remain undetected due to the completeness of inquiline control of the gall phenotype. This possibility is suggested by the fact that *Synophrus* can be abundant even where *A. burgundus* is unknown. Recent evidence suggests that multiple gallwasps have cryptic sexual generations that are morphologically indistinguishable or very similar to *Andricus burgundus* (Stone *et al.* 2008) and these may also serve as hosts for *Synophrus* species.

*Ufo*. *Ufo cerroneuroteri*, known from Taiwan only, was reared exclusively from the spangle galls of the asexual generation of *Cerroneuroterus vonkuenburgi* (Dettmer), while *U. nipponicus*, known from Japan, was reared from spangle galls of asexual generations of *Cerroneuroterus monzeni* (Dettmer) and *C. vonkuenburgi*, and also from asexual galls of *Trichagalma acutissimae* (Monzen). A few wasps emerged from leaf galls of *Andricus kunugifoliae* (Shinji) [for the current status of this species see Abe *et al.* 2007] (Melika *et al.* 2012).

## **Plant host associations of oak cynipid inquilines**

The Fagaceae has its centre of generic diversity in Southeast Asia, and it was thought that the Cynipini only attack a relatively small group of predominantly temperate taxa within this diverse family. Almost all oak gallwasps, which with the majority of *Ceroptres* and *Synergus* complex inquiline species are associated, induce galls on oaks, species in the genus *Quercus* subgenus *Quercus*, and within it attack all four sections of oaks: *Quercus sensu stricto*, *Lobatae*, *Cerris* and *Protobalanus* (see the chapter on Plant hosts of oak cynipid inquilines). Gallwasps attack all of these sections, however, with the exception of the host-alternating species, they attack only closely related members of a single oak section (Cook *et al.* 2002). In North America, for example, the gallwasp faunas of white and red oaks are completely distinct, and no gallwasps attack species in both groups (Cornell 1985, 1986, Abrahamson *et al.* 1998, Melika and Abrahamson 2002). Kinsey's surveys of the Nearctic oak gallwasp fauna found host associations to be

strongly conserved within large groups of genera. For example, all 96 species recognised as belonging to the genus *Cynips* L. are associated only with oaks in *Quercus sensu stricto* (Kinsey 1936). With the exception of the host-alternating species and few others, the same specificity is seen on the two oak sections (*Cerris* and *Quercus sensu stricto*) native to the Palaearctic (Stone *et al.* 2002). Nearly all known oak cynipid inquilines associate with gallwasps on all four sections of *Quercus* subgenus *Quercus*.

Two gallwasp species are known to attack the two endemic western US *Chrysolepis* (*Ch. chrysophylla* and *C. sempervirens*): *Dryocosmus castanopsidis* (Beutenmueller) from Oregon and California (Burks 1979), and *Dryocosmus rileypokei* Morita & Buffington also from California (Buffington and Morita 2009). Only one inquiline species, *Synergus castanopsidis* was reared from *D. castanopsidis* galls (Beutenmüller 1918, Pujade-Villar and Melika 2005); no other inquilines are known to associate with *Chrysolepis*.

A single cynipid, *Andricus mendocinensis* Weld, galls *Notholithocarpus densiflorus* in Mendocino County, California (Burks 1979). No inquilines were described yet which are known to associate with *Notholithocarpus*.

*Dryocosmus kuriphilus* (Yasumatsu), one of very few economically important gallwasps, attack different species of chestnuts, *Castanea*. Outbreaks of this species, native to China, have caused serious damage to local chestnut industries following their introduction to Japan, Korea, the United States and Europe (Payne *et al.* 1975, Kato and Hijii 1993, Gibbs *et al.* 2011). Only a single female *Synergus* sp. was reared from *D. kuriphilus* in Japan (Ôtake *et al.* 1982), which might emphasize the extreme rarity of inquilines in this gall or it is a false data due to a non-accurate rearing technique.

Despite the significance of *Quercus* subgenus *Cyclobalanopsis* in Asia, only a handful of gallwasps were known to induce galls on them: six unnamed cynipid species were reported that depend on species of *Cyclobalanopsis* in Japan (Yukawa and Masuda 1996). Recent research in the Eastern Palaearctic and Oriental region (Japan, China and Taiwan), however, showed that the diversity of cynipids galling *Quercus* subgenus *Cyclobalanopsis* and also *Castanopsis* and *Lithocarpus* is high, a new genus, *Cycloneuroterus* Melika & Tang with new species, number of new *Dryocosmus* species were described revealing the high diversity of cynipid gallwasps and their inquilines in this region (Ide *et al.* 2010, 2012, Melika *et al.* 2010, 2011, Tang *et al.* 2009, 2011a,b, 2012a,b).

**Ceroptres.** *Ceroptres clavicornis* has been reared from galls on section *Quercus* oaks (white oaks) (Askew *et al.* 2012, *in press*) while *C. cerri* attacks galls on section *Cerris* oaks only, including *Quercus cerris* and the Mediterranean evergreen species *Q. ilex*, *Q. coccifera* and *Q. suber* (Pujade-Villar *et al.* 2003, Melika 2006). There are some confusing records for the both western palaeartic

species when they are mentioned in galls from other oak sections, however, those records must be confirmed and might be misidentifications.

Two eastern palaeartic *Ceroptres*, *C. kovalevi* and *C. masudai*, are associated with galls on white oaks only, *Q. crispula*, *Q. dentata*, *Q. mongolica* and *Q. serrata* (Abe 1997, Abe *et al.* 2007, GM, personal data). Plant host associations of two species described from China are unknown (Wang *et al.* 2012).

The nearctic *Ceroptres* species showed no preference toward a particular oak section and were reared from cynipid galls associate with white (10 species) and red (four species) oaks, one species, *C. montensis*, known from California only, was reared from the galls on the Protobalanus section of oaks (Weld 1952).

Thus, *Ceroptres* is associated with all four sections of *Quercus* subgenus *Quercus* and showed no host plant preference, however, no *Ceroptres* species are known to associate with *Quercus* subgenus *Cyclobalanopsis* and oak related genera, *Castanopsis*, *Castanea*, and *Lithocarpus*.

**Synophrus.** All seven known *Synophrus* species are associated with section Cerris oaks: *Q. cerris* throughout Europe, *Q. trojana* in northern Greece, *Q. ithaburensis* in the Middle East, *Q. brantii*, *Q. castaneifolia* and *Q. libani* in Iran, *Q. suber* in North Africa (Pénzes *et al.* 2009). In this way, one of the early main lineages is associated with section Cerris (Fig. 17).

**Saphonecrus and Ufo.** Phylogenetic reconstruction, proposed in this review, divided *Saphonecrus* into several clades (Fig. 17). Three western palaeartic lineages of *Saphonecrus* are associated with different sections of *Quercus* subgenus *Quercus*: (i) “undulatus” group (*S. haimi*, *S. irani* and *S. undulatus*) with Cerris oaks; (ii) “barbotini” (*S. barbotini* and *S. gallaepomiformis*) group with Cerris section, Ilex subgroup, and (iii) “connatus” (*S. connatus* and two undescribed eastern palaeartic species) with *Quercus* section Quercus. The latter is the second early lineage, associated with section Quercus. Two nearctic *Saphonecrus* species are associated with section Lobatae oaks, one with *Quercus* section Quercus s.s., for one species plant host associations are unknown and they were not included yet into any phylogenetic reconstructions. From 13 described eastern palaeartic and oriental *Saphonecrus* species for 7 species plant host associations are unknown (Table 5).

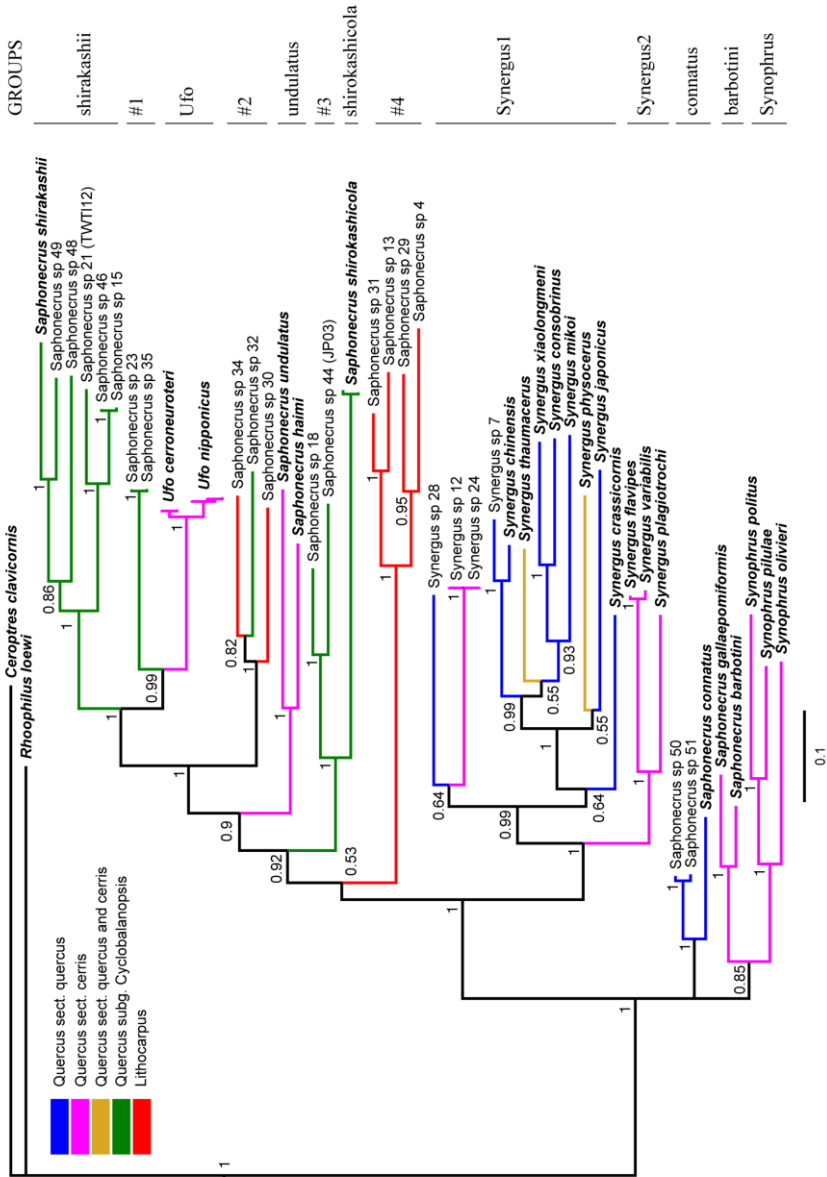


Figure 17. Plant host associations of the Synergus complex of species. For details of phylogenetic reconstruction see Fig. 11. Host associations are shown by colours.

Two *Andricus* species described from Japan on *Q. glauca* by Shinji (1940, 1941) have been regarded as inquilines (Yukawa and Masuda 1996). Wachi *et al.* (2011b) erroneously put them into genus *Ufo*, where from they were moved to *Saphonecrus* (Melika *et al.* 2012). Till now, these are the only two described eastern palaeartic *Saphonecrus* species known to associate with *Cyclobalanopsis*: *S. shirakashii* (Japan and Taiwan) with *Q. (Cyclobalanopsis) glauca* and *Q. (C.) globosa*, while *S. shirokashicola* (also known from Japan and Taiwan) with *Q. (C.) glauca* and *Q. (C.) longinux* (Melika *et al.* 2012). *Saphonecrus excisus* is the only species known to associate with *Lithocarpus elegans* (= *Q. spicata*) (Dalla Torre and Kieffer 1910). *Saphonecrus hupingshanensis*, is the only species known to associate with *Castanopsis carlesii* (Liu *et al.* 2012). *Saphonecrus yukawai* is associated with section Cerris oaks (Wachi *et al.* 2011a). A large number of *Saphonecrus* and near *Saphonecrus* species from the Eastern Palearctic and Oriental Region (Taiwan) are under description and their plant host associations are quite interesting (Fig. 17).

*Saphonecrus* species associated with *Quercus* subgenus *Cyclobalanopsis* are divided into four clades: “shirakashii”, “saphonecrus #1”, “saphonecrus #3”, and “shirokashicola”. “Shirakashii” clade with *Saphonecrus shirakashii* and 5 undescribed species from Taiwan and “saphonecrus #1” with 2 undescribed species from Taiwan form distinct groups. These groups are separated from “saphonecrus #3” and “shirokashicola” clades, which might suggest that at least two or three host plant shifts onto *Cyclobalanopsis* occurred during the evolution of the group. Alternatively, this pattern can be explained by host shifts from *Cyclobalanopsis* toward other hosts assuming *Cyclobalanopsis* host for the common ancestor of the clade between “shirokashicola” and “shirakashii” (Fig. 17). The “saphonecrus #2” clade, which includes also undescribed species from Taiwan, is associated with *Cyclobalanopsis* and *Lithocarpus*. Host associations of these species must be checked, misidentification of host plants is possible, thus any conclusions would be premature.

The phylogenetic position of *Ufo* shows a clear indication for host shift between *Quercus* subgenera. *Ufo* species are associated with section Cerris oaks only: *Q. acutissima* in Japan, *Q. variabilis* in Japan, Korea and Taiwan (Melika *et al.* 2012). Considering the *Ufo*, “saphonecrus #1” and “shirakashii” clade only, shift from *Cyclobalanopsis* to Cerris is the most parsimonious interpretation. The phylogenetic position of “undulatus group” may provide a further example. Finally, the “saphonecrus #4” clade, which includes 4 undescribed Taiwanese species, associate with *Lithocarpus* species only, which suggests relatively early host shift onto this host genus within the third main clade.

We have to emphasize that in between undescribed Taiwanese *Saphonecrus* and near *Saphonecrus* species mentioned until now (the clades between „saphonecrus #4” and „shirakashii”, Fig. 17) there are no lineages

which associate with *Quercus* subgenus *Quercus*. This suggests a deeper division among *Quercus* subgenus *Quercus* sections comparing to the levels of subgenera (*Quercus* and *Cyclobalanopsis*) or even genera (*Lithocarpus* and *Quercus*). However, our data set can not be considered as representative for going into further details of this question.

Except *S. hupingshanensis*, no other *Saphonecrus* species are known to associate with galls on *Castanopsis* (Liu *et al.* 2012). Species from only two genera of gallwasps, *Cycloneuroterus* and *Dryocosmus*, described from Taiwan and Japan, are associated with *Cyclobalanopsis* and *Lithocarpus* (Tang *et al.* 2011a,b, Ide *et al.* 2012). Recently new *Cycloneuroterus* species from Taiwan and oriental China were found to associate with *Castanopsis* species (under description), however, no inquilines were reared from those galls, while inquilines in *Cycloneuroterus* and *Dryocosmus* species which associate with *Cyclobalanopsis* and *Lithocarpus* are quite common. An interesting observed peculiarity of *Saphonecrus* and near *Saphonecrus* species from Taiwan and oriental China is that all species associate with hosts (*Cycloneuroterus* and *Dryocosmus*) which inducing galls on *Cyclobalanopsis*, *Lithocarpus* and *Castanopsis*, while those species never were reared from galls of *Andricus*, *Cerroneuroterus*, *Latuspina*, *Plagiotrochus*, and *Trichagalma* which associate with *Quercus* subgenus *Quercus* species (T.C-T, personal data). In the latter galls, *Synergus* and *Ufo* inquilines species were found only.

***Synergus*.** The host plant associations of the western palaeartic *Synergus* species are well-known. The majority of *Synergus* species are associated only with deciduous oaks in the section *Quercus* while part of them entirely or predominantly associated with oaks in the section *Cerris*. Two European species, *S. plagiotrochi* and *S. ilicinus* appear to be specific to Mediterranean evergreen species in the oak section *Cerris* (*Q. ilex*, *Q. suber* and *Q. coccifera*); *S. synophri* is specific to *Q. suber*, further four species, *S. dacianus*, *S. flavipes*, *S. consobrinus* and *S. variabilis*, are associated with *Q. cerris* and/or further east with *Q. brantii* and *Q. castaneifolii* (Sadeghi *et al.* 2006). There is a clear split between *Synergus* faunas associated with the oak sections *Cerris* (*Q. cerris*, *Q. coccifera*, *Q. ilex* and *Q. suber*) and *Quercus* (*Q. canariensis*, *Q. faginea*, *Q. petraea*, *Q. pubescens* and *Q. robur*) (Fig. 17). Within the oak section *Quercus*, there is a further split between faunas associated with the marcescent (semi-deciduous) Iberian and North African oaks (*Q. pyrenaica*, *Q. faginea* and *Q. canariensis*) and faunas associated with the more broadly distributed deciduous oaks. This split is congruent with the known taxonomic and phylogenetic relationships between these groups (Manos *et al.* 1999). However, the split between “*Synergus* 2” (*S. flavipes*, *S. variabilis* and *S. plagiotrochi*) and “*Synergus* 1” (all other eastern and mainly western palaeartic species) groups on Fig. 17 probably does not reflect strict track in the plant host associations. Three



species in “Synergus 2”, limited to the Western Palaearctic, associate exclusively with the section Cerris, while species in “Synergus 1” – mainly with section Quercus oaks. Some species in “Synergus 1” (e.g. *S. consobrinus*) and two species in a separate subclade Synergus sp. 28, 12, 24, Synergus sp. 12 and Synergus sp. 24, were reared from galls of *Trichagalma formosana* on *Q. variabilis* in Taiwan (section Cerris oaks) while Synergus sp. 28 from section Quercus oaks. Host plant associations in the eastern palaearctic *Synergus* species are less known and very limited data is available.

Our knowledge of the nearctic and neotropic *Synergus* fauna is very superficial. All species are known to associate with one or few gallwasp species which induce galls on the same oak sections. However, data on gallwasp and plant hosts of *Synergus* species is very fragmentary, based mainly on original species descriptions only. Six species are known to associate with the section Protobalanus, near 60% of species, which for the host plant associations are known, are inquilines in galls on white oaks, and around 40% of species are associated with red oaks. Thus, whether there is the same split between species associate with the three sections of oaks, Quercus s.s., Lobatae and Protobalanus, or they can develop in galls on different oak sections needs further research.

There is an evidence for very strong evolutionary conservatism of gallwasp host plant associations at the level of sections within the oak genus *Quercus* L. Recent analyses primarily of Western Palaearctic oak gallwasps have revealed a deep phylogenetic divide between gallwasp taxa galling oaks in the section Cerris on one hand and those galling oaks in the sections Quercus and the nearctic section Lobatae on the other (Cook *et al.* 2002; Ács *et al.* 2007; Liljeblad *et al.* 2008; Stone *et al.* 2009). No doubts that distantly related oaks and related genera commonly support very different gallwasp communities. As a result, grouping of oak species on the basis of similarity in their gallwasp faunas closely matches the phylogenetic relationships between oak species and oaks and other related genera of Fagaceae. The same pattern is seen in the oak host associations of inquiline cynipids (Fig. 17). The plant host associations of inquilines seems to be more important in the biogeography of inquilines than the gallwasp host associations, however, further detail research is necessary to make undoubtfull conclusions.

## Conclusions and future directions

Many aspects of the biology, taxonomy and systematics of the oak associated inquiline genera, especially *Ceroptres*, *Synergus* and *Saphonecrus*, remain unanswered. Little is known about the host gallwasp and host plant associations, host preferences and a real taxonomic assignment of the nearctic species. Detailed research in the taxonomy and systematics of the nearctic species might cardinaly change our current understanding of the group.

Novel approaches are allowing advance in the systematics of the group. Integrative taxonomy and molecular phylogenetics are crucial tools to understand evolution of inquilines including history and biogeography, it will help to understand how the inquilines spread all over the world, how they colonized different plant hosts. Involving samples from the Eastern Palaearctic and the Oriental Region, many new hypotheses are established. Most notably, does the plant host shifts within inquilines rare evolutionary events, like in gallwasps, or they occur much more frequently? All these questions are awaiting answers.

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