Eastern Palearctic oak cynipid inquilines (Hymenoptera: Cynipidae: Synergini) and associated gallwasps (Hymenoptera: Cynipidae: Cynipini)

Ph.D. thesis

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1. INTRODUCTION

1.1. Cynipid gallwasps

Cynipidae lies within the superfamily Cynipoidea of the Hymenoptera, which includes approximately 3,000 described species (Fergusson 1995, Ronquist 1999). With the exception of the Cynipidae and some gall-inhabiting inquiline genera in Figitidae, the cynipoids are all parasitoids, and previous studies suggested that the cynipid gallwasps have evolved from parasitoid ancestors (Ronquist 1994, 1999). Cynipid gallwasps (Hymenoptera: Cynipidae) induce some of the world's most visually striking, and structurally complex plant galls. Approximately 1,440 cynipid gallwasp species were recognized (Liljeblad & Ronquist 1998, Ronquist 1999, Ronquist & Liljeblad 2001, Nieves-Aldrey 2001, Melika 2006), increased considerably recently, although Nordlander (1984) has estimated that the actual number is between 3,000 and 6,000. Ronquist & Liljeblad (2001) hypothesized that the gallwasps arose in Eurasia, around the Black Sea, and that the genera *Eschatocerus* (gall inducers on *Acacia* and *Prosopis*) and *Rhoophilus* (inquilines on *Rhus* galls) spread later to South America and South Africa, respectively. However, recent results may suggest alternative hypothesis, and as such the biogeographical history of the basal Cynipidae is still not clear (Nylander *et al*. 2004, Ronquist *et al.* 2015).

Cynipids are divided into two main trophic groups: the gall inducers, and the gall-associated inquilines. Inquilines develop in galls but can not induce them, except of few *Synergus* species have not lost the capability to induce galls (Csóka *et al*. 2005). In general, inquilinism is a form of cleptoparasitism, usually considered to represent a unilaterally beneficial relationship that benefits only the inquiline (Askew 1984, Ronquist 1994, 1999). This biological division is moderately reflected in the higher-level taxonomy of Cynipidae that has been changed recently. Instead of 8 tribes recognized earlier, the family is divided into 12 tribes (Ronquist *et al*. 2015) (Table 1).

Most of the described species of Cynipidae are gall inducers (Table 1.). However, more than 220 species, classified traditionally into ten genera and placed to four tribes recently (Table 1), develop as inquilines inside galls of other cynipids (Pujade-Villar *et al*. 2003, Nieves-Aldrey & Medianero 2010, Bozsó 2015, Bozsó *et al*. 2014, 2015, Ronquist *et al.* 2015). Inquiline cynipids feed obligately on plant tissues within developing galls, and to some extent, stimulate the development of tissues characteristic to galls. Our research focuses particularly on inquilines that attack hosts in the Cynipini (oak gall wasps) associated to Fagaceae host plants. Some synthesis based on published data has also been done on oak gall inducers.

Table 1. Classification, diversity and host associations of Cynipidae
(after Ronquist *et al.* 2015, genera and species numbers updated by Sz. Schwéger)

Tribes	**Genera**	**Species**	**Hosts**	**Distribution**
Cynipini	41	954	Gall inducer on Fagaceae (*Quercus*, *Castanea*, *Castanopsis*, *Chrysolepis* and *Lithocarpus*)	Holarctic, Neotropical, Oriental
Diplolepidini	2	55	Gall inducer on *Rosa* (Rosaceae)	Holarctic
Pediaspidini	2	2	Gall inducer on *Acer* (Aceraceae)	Palearctic
Eschatocerini	1	3	Gall inducer on *Acacia*, *Prosopis* (Fabaceae)	South Neotropical
Qwaqwaiini	1	1	Gall inducer on *Scolopia* spp. (Salicaceae)	Afrotropical (South Africa)
Paraulacini	2	6	Inquilines or parasitoids in chalcidoid galls (Pteromalidae) on *Nothofagus* spp. (Nothofagaceae)	South Neotropical
Aylacini sensu stricto	3	9	Gall inducers on *Papaver* spp. (Papaveraceae)	Palearctic
Aulacideini	9	78	Gall inducers on Asteraceae, Lamiaceae, Valerianaceae and the tribe Fumarioideae (Papaveraceae)	Holarctic
Phanacidini	4	34	Gall inducers on several genera of Asteraceae, rarely on *Phlomis* (Lamiaceae) and *Eryngium* (Apiaceae)	Palearctic, one species South Afrotropical (possibly introduced). Introduced in South America and Australia
Diastrophini	4	43	Gall inducers in galls on *Rubus* spp. and *Potentilla* spp. (Rosaceae), rarely on *Smilax* (Smilacaceae), and inquilines in cynipid galls on *Rubus* spp. *Synophromorpha*) and *Rosa* spp. (Rosaceae) (*Periclistus*)	Holarctic and Neotropical (one species)
Ceroptresini	1	24	Inquilines in galls induced by Cynipini, one genus, *Ceroptres*.	Holarctic
Synergini sensu stricto	7	155	Inquilines in cynipid galls on Fagaceae genera, *Quercus* (*Agastoroxenia*, *Lithosaphonecrus*, *Saphonecrus*, *Synophrus*, *Synergus*, *Ufo*). One genus (*Rhoophilus*) is an inquiline Cecidosidae (Lepidoptera) galls on *Rhus* spp. (Anacardiaceae)	Holarctic, Neotropical, Oriental, Oceanian
Cynipidae	77	1364		

1.2. Host plants of oak gallwasps

Oak gallwasps, inducers and inquilines, are intimate parasites of trees belong to the familiy Fagaceae. In order to understand their evolution and recent distribution the knowledge of their host plant associations is important. Fagaceae is divided into two subfamilies: Fagoidea, with *Fagus* and *Quercus* genera, and Castaneoidea, with insect-pollinated *Castanea*, *Castanopsis*, *Chrysolepis*, *Lithocarpus* and *Notholithocarpus*, all five of which serve as hosts for Cynipini (Govaerts & Frodin 1998, Manos *et al*. 2008). The number of known species within Fagaceae is contraversial; from 900 to *ca*. 1,050 species are mentioned (Govaerts & Frodin 1998, Oh & Manos 2008). No gallwasps are known from some Fagaceae genera. The family Fagaceae formerly included the southern beeches of the genus *Nothofagus* distributed in South America 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 documented in Chile and Argentina, however no Cynipidae are known on this genus from Australasia (Nieves-Aldrey *et al*. 2009). Gallwasps are mainly associated to the following six genera of Fagaceae.

Castanea (chestnuts) genus is represented by 8–10 species, native to temperate regions of the Northern Hemisphere, with two known gallwasp species, *Dryocosmus kuriphilus* and *D. zhuili* (Zhu *et al*. 2015). No cynipid inquilines were reared yet from these galls, however, recently *Synergus castaneus* was described from China as the first cynipid inquiline species associated with *Castanea* galls (Bernardo *et al*. 2013).

Castanopsis (chinquapin oaks) is a genus which involves about 120 species, all of which are restricted to eastern Asia (Oh & Manos 2008). Recently a number of new gallwasp and cynipid inquiline species were described from *Castanopsis* (Tang *et al*. 2016a, Schwéger *et al*. 2015a, b).

Chrysolepis (golden chinquapin oaks) is a small genus, endemic to the western United States, with two species, *Ch. chrysophylla* and *Ch. sempervirens.* Few inquilines associate with few cynipid gallwasps develop on *Chrysolepis* are known (Burks 1979).

Lithocarpus (stone oaks) is a large genus, distributed in east and southeast Asia, with more than 300 species (Govaerts & Frodin 1998). Recently this genus has been shown to host Cynipini (Tang *et al*. 2011a) and cynipid inquilines (Bozsó *et al.* 2014).

Notholithocarpus (tanbark oaks or tanoaks) with only one known North American species, *N. densiflorus*, only recently was established (Govaerts & Frodin 1998, Manos *et al*. 2008, Oh &

Manos 2008). It is an evergreen tree, native to the western United States. 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 (Burks 1979) including inquilines (Bozsó *et al.* 2015).

Majority of Cynipini induce galls on members of a large genus *Quercus* which is divided into two long-established subgenera – the strictly Asian subgenus *Cyclobalanopsis* and the more widespread subgenus *Quercus* (Camus 1936-54, Nixon 1989, 1993, Govaerts & Frodin 1998, Manos *et al*. 1999). Many of them are serving as host for inquilines, too. The subgenus *Quercus* is divided into discrete sections (Govaerts & Frodin 1998), including Lobatae (the red oaks), Protobalanus (the golden cup or intermediate oaks), Quercus sensu stricto (the white oaks), and Cerris. The latter comprise the Ilex group, too. 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 Palearctic. Worldwide, there are 531 recognised oak species (according to Govaerts & Frodin 1998), but generally reported as between 300 and 600 (Hubert *et al.* 2014). 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). The Palearctic supports *ca*. 170 species, with *ca*. 130 species in the EP and only 29 species in the WP (Govaerts & Frodin 1998). The oak sections Cerris and Quercus sensu stricto are widespread in the EP, and the regional richness of oaks – with 32 species in China (Linkuo & Tao 1998), at least 17 in Himalayan India, Nepal and Bhutan (Negi & Naithani 1995), and 6 in Japan (Ohwi 1961) – exceeds the Western Palearctic's 29 species.

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 & 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 *et al.* 2001), althought the placement of *Cyclobalanopsis* is equivocal (Hubert *et al.* 2014). 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 (Zhou 1992, 1993, Manos & 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. Nevertheless, althought there are clear host specific clades (Ács *et al.* 2010, Pénzes *et al.* 2012, Bozsó *et al.* 2014), the general pattern is to be explored.

1.3. Synergini sensu stricto

According to the earlier classifications, *Synophromorpha* Ashmead, *Periclistus* Förster, *Ceroptres* Hartig, *Agastoroxenia* Nieves-Aldrey & Medianero, *Lithosaphonecrus* Tang, Melika & Bozsó, *Saphonecrus* Dalla Torre & Kieffer, *Synophrus* Hartig, *Synergus* Hartig, *Ufo* Melika & Pujade and *Rhoophilus* Mayr, were classified within the polyphyletic tribe Synergini (Burks 1979, Ronquist 1999, Pénzes *et al.* 2012, Ronquist *et al.* 2015). A world-wide review of all cynipid inquilines was given in Pénzes *et al*. (2012). Recently, *Periclistus* and *Synophromorpha* were moved to the newly established Diastrophini tribe; a new tribe Ceroptresini was established for the *Ceroptres* genus, while the rest 7 genera, *Agastoroxenia*, *Lithosaphonecrus*, *Saphonecrus*, *Synophrus*, *Synergus*, *Ufo*, *Rhoophilus*, were put into the tribe Synergini sensu stricto (Ronquist *et al.* 2015, Table 1).

Phylogeny of the oak gallwasp inquilines, based mainly on the Eastern and Western Palearctic species, has long been controversial, especially in the Synergini sensu stricto genera (Ács *et al*. 2010). Table 2 shows the number of described species including all the newly described *Synergus* and *Saphonecrus* (Schwéger *et al*. 2015a, b; Results section).

The number of known Synergini species is unevenly distributed among the zoogeographical regions (Table 2). This clearly reflects the differences in the intensity of sampling. Western Palaeartic (WP) is the best known. The Synergini fauna of Eastern Palearctic (EP) is being explored recently. It is expected to be more diverse and probably many new species will be described in the future. In part, this expectation can be explained by the diversity of potential host plant (detailed below), compared to the WP. Tropical regions are poorly studied.

Table 2. The world distribution and species richness of Synergini sensu stricto genera (WP, Western Palearctic, EP, Eastern Palearctic, OR, Oriental Region, NA, Nearctic, NT, Neotropical Region, ET, Ethiopian Region).

Genera	Hosts	WP	EP	OR	NA	NT	ET	World
Agastoroxenia Nieves-Aldrey& Medianero, 2010	Oak cynipid galls	–	–	–	–	1	–	1
Lithosaphonecrus Tang, Melika & Bozsó, 2013	Oak cynipid galls	–	4	2	–	–	–	6
Synergus Hartig, 1840	Oak cynipid galls	30	19	–	55	14	–	118
Saphonecrus Dalla Torre & Kieffer, 1910	Oak cynipid galls	6	25	2	3	–	–	36
Synophrus Hartig, 1843	Oak cynipids galls	7	–	–	–	–	–	7
Ufo Melika & Pujade, 2005	Oak cynipid galls	–	3	1	–	–	–	4
Rhoophilus Mayr, 1881	*Rhus* galls	–	–	–	–	–	1	1
Total:		**43**	**48**	**5**	**58**	**15**	**1**	**170**

Inquilines which attack hosts in the gallwasp tribe Cynipini (gall inducer oak gallwasps) include six genera, *Agastoroxenia*, *Saphonecrus*, *Synergus*, *Synophrus*, *Ufo*, *Lithosaphonecrus*, earlier named as the *Synergus* complex of genera (Pénzes *et al*. 2012). One genus, *Rhoophilus*, with one species, *Rh*. *loewi* Mayr, known from South Africa, is an inquiline in Cecidosidae (Lepidoptera) galls on *Rhus* spp. (Anacardiaceae). It was recently examined in details (van Noort *et al*. 2007). Probably all seven genera form together a distinct monophyletic lineage (Ronquist *et al*. 2015) and *Rhoophilus* generally recovered as the sister taxon of all others (e.g. Ács *et al.* 2010, Ronquist *et al.* 2015). The morphological taxonomy of Synergus complex has been studied in details (Mayr 1872; Wiebes-Rijks, 1979; Nieves-Aldrey & Pujade-Villar 1985, 1986; Pujade-Villar & Nieves-Aldrey 1990, 1993; Liljeblad & Ronquist 1998; Liljebald *et al*. 2008; Pujade-Villar *et al*. 2003, Melika 2006; Melika *et al.* 2012; Bozsó *et al.* 2015) and (i) supported the differentiation of these two lineages, and (ii) showed that five genera, *Agastoroxenia*, *Saphonecrus, Synergus, Synophrus* and *Ufo* morphologically differs from *Ceroptres* .

Inconsistencies in the taxonomy of gallwasps were revealed by the DNA sequence-based studies. For example the presence of cryptic species, independently evolving lineages that are morphologically indistinguishable, had been demonstrated in many times (Ács *et al*. 2010, Kaartinen *et al*. 2010). Consequently it is becoming increasingly common to supplement morphological identifcation with molecular methods such as DNA barcoding (Hebert *et al.*

2003). Recently obtained data suggest that the variability of the widely-used region of the mitochondrial *coxI* gene together with *cytb* and the nuclear 28S D2 sequences can be used to define clusters of samples (MOTU, Molecular Operational Taxonomic Unit, Blaxter *et al.* 2005.) within the *Synergus* complex of genera (Ács *et al*. 2010). However, comparison of morphology-based species identification with MOTU designations revealed substantial discordance (explained below). The application of morphological and molecular characters together helped us to establish a more reliable taxonomy for *Synophrus* (Pénzes *et al*. 2009), *Synergus* (Ács *et al.* 2010), *Ufo* (Melika *et al*. 2012), *Saphonecrus* (Bozsó *et al.* 2014) and *Lithosaphonecrus* (Bozsó 2015, Bozsó *et al*. 2015).

Synergus Hartig 1941

Thirty *Synergus* species are known from the Western Palearctic (Pujade-Villar *et al.* 2003, Pénzes *et al*. 2012), which from about 80% of species was involved into a DNA sequence-based delimitation and phylogenetic analysis (Ács *et al.* 2010). The analyses supported monophyly of the genus *Synergus* but rejected the traditional classification, namely the monophyly of the two sections within *Synergus* (Section I and Section II, Mayr 1872), and the monophyly of some morphospecies (*S. hayneanus, S. pallipes*, *S. umbraculus*, *S. flavipes*). The results showed that some distinct WP *Synergus* morphospecies belong to the same MOTU, while some morphospecies, e.g. *Synergus umbraculus*, *S. hayneanus*, revealed cryptic species. In other words some recognised WP *Synergus* species correspond to MOTUs, others clearly do not. The sequence data was unable to discriminate between *S. gallaepomiformis, S. pallicornis, S. pallidipennis* and *S. pallipes*. All these results suggested that some WP *Synergus* morphospecies should be revised.

Before our work 12 valid species of *Synergus* were known from the Eastern Palearctic (Sadeghi *et al*. 2006, Bernardo *et al*. 2013, Abe *et al*. 2011, Pujade-Villar *et al*. 2014a, b, c). While all known WP *Synergus* species associate with galls on *Quercus* (subgen. *Quercus* sections Quercus and Cerris) precise host associations were known only for a few Eastern Palearctic *Synergus* species before 2008 (Abe 1990, 1992a, Abe *et al*. 2007). Large number of *Synergus* specimens was reared during 2008-2012 from different hosts which associate with *Quercus* and *Quercus* related genera within Fagaceae. The taxonomic assignment of undescribed species from Japan, the Far East Russia and Taiwan and the re-appraisal of known EP species with a preliminary phylogenetic placement has been done (Schwéger *et al*. 2015a). However, taxonomic status of Nearctic *Synergus* is still equivocal (Pénzes *et al.* 2012).

Saphonecrus Dalla Torre, 1910 and *Lithosaphonecrus* Tang, Melika & Bozsó, 2013

Our knowledge about the taxonomic diversity of *Saphonecrus* has been expanded recently, especially in the EP region (Table 2). Before 2008 24 species of *Saphonecrus* were known worldwide covering the Palearctic, Nearctic and the Oriental region (Pénzes *et al*. 2012, Bozsó *et al*. 2014). The six WP species are associated mainly with galls on section Cerris oaks, including Mediterranean evergreen oaks (*Quercus ilex* L., *Q. suber* L., *Q. coccifera* L.) and *Q. cerris* L. in Central Europe, while some are associated with galls that develop on white oaks (section Quercus, e.g. *Q. petraea* Liebl., *Q. robur* L. in Central Europe (Schwéger *et al.* 2015b). In 2007, seven *Saphonecrus* species were listed for the EP (Abe *et al*. 2007) and two species, *S. serratus* Weld and *S. areolatus* Weld, were known from the Oriental Region (Weld 1926). Recently new species were described from Japan and China (Liu *et al.* 2012, Wang *et al.* 2010, Wachi *et al.* 2011b, Pujade-Villar *et al*. 2014a, c). The most complete molecular phylogenetic reconstruction of *Saphonecrus* with examination of known species was recently proposed with involving new lineages from Japan, Russia, China and Taiwan (Pénzes *et al*. 2012, Melika *et al.* 2012, Bozsó *et al*. 2014, 2015). The taxonomic assignment of new species and the re-appraisal of all known *Saphonecrus* species worldwide based on morphological and molecular characters was evaluated by us (Schwéger *et al*. 2015b). Four *Saphonecrus* species listed for the Nearctic (Burks 1979), they possess some non-typical character states for *Saphonecrus*, and thus their taxonomic assignment is questioned.

New genera, *Lithosaphonecrus* Tang, Melika & Bozsó and *Lithonecrus* Nieves-Aldrey & Butterill, and number of new species within genera of Synergini have recently been described (Bozsó *et al*. 2014, 2015; Melika *et al*. 2005, 2007, 2012; Pénzes *et al*. 2009; Nieves-Aldrey & Butterill 2014) which were examined in details by us and as the result some genera and species were synonymized (Schwéger *et al.* 2015b).

1.4. Origin and evolution of cynipid inquilines; phylogeny of Synergini sensu stricto

Ronquist *et al.* (2015) distinguished three major possible scenarios for the origin of cynipid inquilines. Several previous studies suggested the “gall inducers first” scenario wherein the inquilines evolved once from herb gallers in the Northern Hemisphere. At first they lost the capability to induce galls and started to parasitize their closest relatives. Then, the inquilines radiated worldwide and parasitized several different Cynipini lineages. They found several phylogenetic evidences which shaded this hypothesis and they supported other scenario is called "multiple transitions" instead of the previous one. It concerned that the first gall inducer cynipids associated with woody hosts in the Northern Hemsiphere and after there have been a multiple transitions between cynipid gallers and inquilines. In this second scenario, inquilines do not form a monophyletic unit and transitions could be host plant specific (e.g. result in separate radiation on Rosaceae and Fagaceae). Third scenario called "inquiline first" wherein the ancestral gallwasp was inquiline, possibly in Southern Hemisphere and the gall inducers evolved independently multiple times in different lineages of inquilines. Further studies are needed worldwide to test these hypotheses.

The phylogeny of Synergini sensu stricto genera recently was investigated. The phylogenetic position of *Synophrus* and *Ufo* has been re-appraised and re-established (Bozsó *et al*. 2014, 2015; Melika *et al*. 2005, 2007, 2012; Pénzes *et al*. 2009; Nieves-Aldrey & Butterill 2014).

1.5. Eastern Palearctic oak gallwasps (Cynipidae: Cynipini)

Oak gallwasps (Hymenoptera: Cynipidae: Cynipini) are by far the most species-rich group of gallwasps, with more than 1,000 known species worldwide (Csóka *et al*. 2005, Ronquist *et al*. 2015). There are only a few Cynipidae (Hymenoptera) reviews on the EP species (Dalla Torre & Kieffer 1910, Abe *et al*. 2007). Both are out of time and since then dozens of new species were described and a large number of nomenclatorial changes have been done. Recently some review papers were published on EP cynipid inquilines (Cynipidae: Synergini) (Pénzes *et al*. 2012) and its genera in Synergini and Ceroptresini. Abe *et al*. (2007) listed all the known EP rose gallwasps (Diplolepidini) and herb gall wasps ("Aylacini"), while the list of oak gallwasps (Cynipini) currently is far from completeness. The Eastern Palearctic as defined here includes Asia east to Iran, the Ciscaucasus (Transcaucasus) and the Ural Mountains. Species known only from more western regions, such as from Iran, the Transcaucasus, Dagestan are not included.

Oak cynipid taxonomy and biology is in a period of rapid advance, both in terms of our understanding of cynipid biology and of resolving taxonomic issues within the Cynipini. New genera, species and generations continue to be discovered in Japan (Ide *et al*. 2010, 2012, 2013, Wachi & Abe 2010), Taiwan (Melika *et al*. 2010, 2011, 2012, 2013, Tang 2015, Tang *et al*. 2009, 2011a, b, 2012a, b, 2016a, b, c), China (Pujade-Villar & Wang 2012, Wang *et al.* 2013, Abe *et al*. 2014a, Pujade-Villar *et al*. 2014a), Vietnam (Abe *et al*. 2014b). In particular, Taiwan and China are areas with high oak (*Quercus* L., subgen. *Cyclobalanopsis* and *Quercus*) and oak relatives' (*Castanea* Miller, *Castanopsis* Miller, *Lithocarpus* Blume) species richness whose cynipid faunas remain little-studied, and future work will certainly reveal further new species.

Table 3. Species richness of the EP oak gallwasps (Cynipini) with their host associations

Genus	Total species number	*Quercus* subgen. *Quercus*	Quercus subgen.Cyclo-balanopsis	*Castanea*	*Castanopsis*	*Lithocarpus*	Unknown host	Species with uncertain status
Andricus Hartig, 1840	16	16	–	–	–	–	–	2
Aphelonyx Mayr, 1881	–	–	–	–	–	–	–	2
Belizinella Kovalev, 1965	2	2	–	–	–	–	–	–
Biorhiza Westwood, 1840	1	1	–	–	–	–	–	–
Callirhytis Foerster, 1869	1	1	–	–	–	–	–	2
Cerroneuroterus Melika & Pujade-Villar, 2009	3	3	–	–	–	–	–	–
Cyclocynips Melika, Tang, & Sinclair, 2013	2	–	2	–	–	–	–	–
Cycloneuroterus Melika & Tang, 2011	17	–	15		1	1	–	–
Cynips Linnaeus, 1758	1	1	–	–	–	–	–	–
Dryocosmus Giraud, 1859	12	2	2	2	4	–	2	2
Latuspina Monzen, 1954	9	9	–	–	–	–	–	–
Neuroterus Hartig, 1840	7	4	1	–	–	–	2	2
Plagiotrochus Mayr, 1881	7	–	5	–	–	–	2	–
Trichagalma Mayr, 1907	3	3	–	–	–	–	–	–
Trigonaspis Hartig, 1840	3	3	–	–	–	–	–	–
Ussuraspis Kovalev, 1965	1	1	–	–	–	–	–	–
TOTAL	**85**	46	25	2	5	1	6	10

All the data on the EP Cynipini fauna is fragmented, published in numerous taxonomic paper (Abe 2006, 2007, Abe *et al*. 2012, 2014a, b, Ide *et al*. 2010, 2012, 2013, Melika *et al*. 2010, 2012, 2013, Tang *et al*. 2009, 2011a, 2011b, 2016a, b, c). Thus our aim was to compile a list of all know EP Cynipini with including also species with uncertain status (*nomena dubia*).

In the Western Palearctic and Nearctic the majority of oak gallwasps associate with oaks of the *Quercus* subgenus *Quercus* (Stone *et al*. 2002, Melika 2006). Recent studies in the Eastern Palearctic have revealed a potentially rich oak gallwasp fauna associate with four Fagaceae genera, *Castanea*, *Castanopsis*, *Lithocarpus*, *Quercus* (subgenus *Quercus* and subgenus *Cyclobalanopsis*) (Abe *et al*. 2014a, b, Ide *et al.* 2010, 2012, 2013, Melika *et al*. 2011, 2013, Tang *et al.* 2011a, b; Melika *et al*. 2011). Numbers of recognised species in each genus of Cynipini are summarised in Table 3. Different host plants were colonized by the representatives of different genera. For instance, species of *Andricus*, *Belizinella*, *Biorhiza*, *Cerroneuroterus*, *Cynips*, *Latuspina*, *Trichagalma*, *Trigonaspis*, and *Ussuraspis*, associate only with *Quercus* subgenus *Quercus*. Number of genera associate mainly with the species of *Quercus* subgenus *Cyclobalanopsis* and only few species of *Cycloneuroterus* and *Dryocosmus* are known to associate with other three oak related genera: two *Dryocosmus* species with *Castanea*, one *Cycloneuroterus* and four *Dryocosmus* species with *Castanopsis*, and one species of *Cycloneuroterus* with *Lithocarpus*.

1.6. Main objectives of the work

My aim is to summarize the taxonomic problems, concerning the EP Synergini and Cynipini fauna, using morphological and molecular data. The Main Objectives:

1. Taxonomic and phylogenetic re-appraisal of Synergini sensu stricto genera; synonymization of some genera and species (Pénzes *et al.* 2012, Schwéger *et al.* 2015a, b).
2. Combining keys for the identification of Synergini sensu stricto genera, with producing necessary colour plates with adequate morphological characters (Pénzes *et al.* 2012).
3. Composing first keys to all EP *Synergus* species and to Palearctic *Saphonecrus* species, with colour plates of adequate morphological characters (Schwéger *et al.* 2015a, b).
4. New EP species of *Saphonecrus* (15 new species were described by us) and *Synergus* (8 new species were described by us), their detailed diagnoses, descriptions, biology, host associations (Schwéger *et al.* 2015a, b).
5. Re-appraisal of all EP *Synergus* species and that of Palearctic *Saphonecrus* species (Schwéger *et al.* 2015a, b).
6. Compilation of the up-to-date complete list of EP Cynipini (unpublished result).

2. MATERIALS AND METHODS

2.1. Synergini sensu stricto

2.1.1. Specimen collection

All the wasps we obtained were laboratory reared from fresh galls collected in different localities in Japan, Russia, China and Taiwan during 2008–2012 (coordinated by Graham N Stone, Univ. Edinburgh, UK). Galls were put into sealed plastic bags during the field work and taken to the laboratory for rearing. Galls collected in Japan, Russia and Taiwan during 2008 were reared at the University of Edinburgh, UK (reared by J. Nicholls); galls collected in later years in Taiwan and China were reared at the National Chung Hsing University, Taichuing, Taiwan (reared by C.-T. Tang). For rearing galls were placed in plastic containers at a room temperature, with square windows cut into the lids and covered with a mesh for the proper ventilation to avoid fungal infection. Containers were checked every day, and wasps that had emerged were aspirated and placed in 99% ethanol for further laboratory processing. All the reared wasps were sent to G. Melika (Plant Health and Molecular Biology Laboratory, National Food Chain Safety Office, Budapest) for further morphological identification. For the host plants identification Lu *et al*. (2006) and Govaerts & Frodin (1998) were used.

2.1.2. DNA extraction, sequencing, alignment and phylogenetics

Adults were preserved in 99% ethanol and stored at -20 °C until DNA extraction. Some specimens, including *Synergus kawakamii* were obtained as dry samples. Genomic DNA was extracted from one to three legs and/or the whole body of adult specimens, following the chelex extraction method presented in Nicholls *et al*. (2010). A fragment of the mitochondrial cytochrome c oxidase subunit I (*coxI*) gene was amplified using the forward primer LCO-1490 (5' GGT CAA CAA ATC ATA AAG ATA TTG G 3') and HCO-2198 (5’ TAA ACT TCA GGG TGA CCA AAA AAT CA 3’) (Folmer *et al*. 1994). A fragment of the D2 expansion segment of the nuclear 28S ribosomal array (28S D2) was amplified using the primers D2 forward (5′-CGTGTTGCTTGATAGTGCAGC-3′) and D2 reverse (5′-TCAAGACGGGTCCTGAAAGT-3′) (Hancock *et al*. 1988). Each 25 µl PCR mix consisted of 0.25 µl of 5U/µl Taq DNA polymerase (Fermentas), 2.5 µl of 10X Taq buffer, 2.0 µl $MgCl_2$ (25 mM), 0.5 µl dNTPs (10 mM), 0.5 µl of each primers (20 pmol), 2.0 µl template DNA, and 16.75 µl purified and distilled water. Cycling conditions were 94°C for 2 minutes, followed by 35 cycles of 94°C for 30 seconds, 45°C (28SD2) or 50°C (*coxI*) for 30 seconds, and 72°C for 45 seconds, with a final step of 72°C for 10 minutes. PCR products were purified from 1% agarose gel using the Millipore Ultrafree-DA DNA extraction kit. PCR products were sequenced directly by MWG-Biotech AG (http://www.mwg-biotech.com) or LGC Genomics Gmbh using Sanger method. Chromatograms were checked by eye using Staden package 2.0 (Bonfield *et al.* 1995). 28S D2 regions were sequenced in both directions, while *coxI* was sequenced only in the forward or both directions. New Synergus haplotypes are deposited in GenBank, under accession numbers KR270530 – KR270560 and KR537436 – KR537438 (detailed below.). Further fully overlapping sequences were downloaded from previous studies of gallwasp inquilines (Synergini) (Ács *et al.* 2010; Pénzes *et al.* 2009; Melika *et al.* 2012; Bozsó *et al.* 2014; Kaartinen *et al.* 2010, Bernardo *et al.* 2013, Nylander *et al.* 2004; detailed below.). *CoxI* sequences were aligned without difficulty using Muscle 3.8.31 (Edgar *et al.* 2004) using the default settings as no gaps were detected. 636 sequence positions were involved as characters in the following phylogenetic analysis. Sequences of the 28S D2 region were aligned using MAFFTX–INS-i version 7.157b using the default settings (Katoh *et al.* 2002, Katoh & Standley 2013) and resulted in 604 sequence positions. Following the alignments, phylogenetic reconstruction was carried out in a Bayesian framework using MrBayes 3.2.4 64-bit parallel version (Ronquist & Huelsenbeck 2003, Altekar *et al.* 2004, Ronquist *et al.* 2012) for the combined coxI+28S D2 dataset. Separate partitions with varying rate and unlinked parameters were defined for D2 and three *coxI* codon positions. For all four partitions, four-by-four nucleotide models were selected and a GTR substitution model space were sampled during the MCMC analyses (nst=mixed option) with gamma distributed rate variation across sites. Default priors were used for all parameters.

Two independent runs were performed with the default MCMC parameters except the following settings: MCMC runs comprised 10 million generations sampled every 1000 generations with 30% considered as burn-in. Sufficient convergence was achieved in the analysis diagnosed by the average standard deviation of split frequencies between the two independent runs (<0.01) and PSRF values (1 with <1% deviation). *Rhoophilus loewi* was used to root the phylogenetic tree (Ács *et al.* 2010).

2.1.3. Morphological descriptions

The terminology used to describe gallwasp morphology follows recent cynipid studies (Melika *et al*. 2010; Liljeblad *et al*. 2008). Abbreviations for fore wing venation follow Ronquist & Nordlander (1989), cuticular surface terminology follows that of Harris (1979). Measurements and abbreviations used here include: F1–F12, 1st and subsequent flagellomeres; POL (post-ocellar line) is the distance between the inner margins of the posterior ocelli; OOL (ocellar-ocular line) is the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; LOL, the distance between lateral and frontal ocelli. The width of the forewing radial cell is measured from the margin of the wing to the Rs vein.

Images of wasp anatomy were produced with a digital Leica DC500 camera attached to a Leica DM2700M compound microscope with using the LAS Store&Recall software, followed by processing in Adobe Photoshop 6.0. Images of adult wasps were produced by Szabina Schwéger (all *Synergus* and *Saphonecrus* species), while some pictures of *Ufo*, *Synophrus* and *Lithosaphonecrus* were taken by Dr. Miklós Bozsó (Plant Health and Molecular Biology Laboratory, National Food Chain Safety Office, Budapest, Hungary). Gall images were taken in the field mainly by Chang-Ti Tang (National Chung Hsing University, Taichung, Taiwan) and Dr. György Csóka (NARIC, Forest Research Institute, Department of Forest Protection, Mátrafüred, Hungary).

The type material is deposited in the following institutions: PHMB, Plant Health and Molecular Biology Laboratory, National Food Chain Safety Office, Budapest, Hungary (curator G. Melika); NCHU, Department of Entomology, National Chung Hsing University, Taichung, Taiwan (curator C.-T. Tang); USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. (curator M. Buffington). Morphological peculiarities are given in Appendix 9.1.

2.2. Oak gallwasps (Cynipidae: Cynipini)

The list of EP Cynipini includes those oak gallwasps (Cynipidae: Cynipini) whose names are (i) valid according to the rules of the International Code of Zoological Nomenclature (1999) (ICZN) and (ii) which were regarded as real biological entities in the literature. The vast majority of the listed species have been collected many times by G. Melika and other co-authors in Schwéger *et al*. (2015a, b) in different parts of the EP (Far East of Russia, Japan, South Korea, China, Taiwan) and research done on those species (taxonomic and/or molecular phylogenetic and/or rearing work) supports their existence as distinct biological units. Rare species listed have also been carefully checked (type material of adult wasps and galls was examined where possible by G. Melika, and the relevant literature was analysed by me). This work is made more difficult by the fact that the types of some species have been lost (for example, some species described by Shinji (1938, 1940, 1941) from Japan). Recent nomenclatorial changes have been taken into account and these mean that some generic names are no longer used. All known literature names for specific species are linked to the currently recognised names under the Synonyms part. There are EP oak gallwasp species names in the literature that, although valid in the strict taxonomic sense, represent uncertain or questionable taxa. Some appeared in the literature only in the original description and have never since been collected or cited. Such species (species names) are also listed as nomina dubia (species with uncertain status) and are given after the valid species list.

Summaries are presented for each species in alphabetical order in Appendix 9.2. in the following format:

Synonyms. All known synonyms are given and, where appropriate, they are attributed to specific generations in the lifecycle. The names of many species have changed since their original description and thus we are listing all known synonyms for each species and generation. The validity of a taxon name according to the International Code of Zoological Nomenclature (ICZN) is based on the priority principle: valid species name is that which was first published. All other later published names that refer to the same species are junior synonyms. Gallwasp nomenclature is unusual in comparison to other insect groups in that in many cases alternate generations of a single biological entity were described as different species or even as members of different genera, and only later found to represent halves of the same lifecycle. In this case, the name of the first generation to be described is the valid name for the species, the second generation's name becoming a junior synonym. So for oak gallwasps the term "synonym" refers both to real synonyms of a known 2-generation species and to synonyms linking alternate generations. We have included not only synonyms, but also all existing name combinations as the generic arrangement of many species has evolved over time.

Lifecycle. We say which of sexual and asexual generations are known for the species, together with any specific literature involved in linking generations.

Geographic distribution. We provide an overview of the updated distribution of each species, and list the countries from which each species has been recorded across the EP.

Host plants. The names used follow the revision by Govaerts & Frodin (1998).

Gall location and structure. The plant part affected by a given gall is described. We describe the structure of the mature gall and, where possible, also summarise changes that take place during gall development. Galls are described as being unilocular (containing a single larval chamber) and multilocular (a single structure containing many larval chambers). Unilocular galls may be solitary or gregarious (many discrete galls clustered together). Some unilocular galls are also able to coalesce into an apparently multilocular structure when they develop in close proximity.

Phenology. Data on the timing of gall development, the frequency and duration of diapause and of the flight periods of the adults are provided.

Similar galls. We describe galls induced by other species that could be confused with the gall in question, and summarise diagnostic characters for their identification.

In Appendix 9.3. the list of EP Cynipini species with uncertain status (*nomena dubia* or *incertae sedis*) is given. A common way for a taxon name to become a *nomen dubium* is loss of the original type material, which prevents revision of the taxon and establishment of synonymy with other taxa.

3. RESULTS

3.1. Synergini sensu stricto

Besides the tribe Ceroptresini, the tribe Synergini sensu stricto comprises inqulines associated mainly with Fagaceae. Table 2 includes currently known 7 genera belong to this tribe with the number of all the newly (*Synergus* and *Saphonecrus*) and recently (*Synophrus*, *Ufo*, *Lithosaphonecrus)* described species (Pénzes *et al*. 2009, Bozsó 2015, Bozsó *et al*. 2014, 2015, Melika *et al*. 2012, Schwéger *et al.* 2015a, b). To keep the integrity of formal descriptions, general comments are given in the Results section, too.

3.1.1. Key to Cynipidae tribes

For the identification of the Cynipidae tribes the next key is proposed, with original colour plates (unpublished). The key follows that of Ronquist *et al*. (2015), with some modifications and simplifications.

Key to Cynipidae tribes

1. Female antenna clavate; last flagellomere wider than penultimate; male antenna with either F2, F3 or both modified; ventral area of gena with 5–9 vertical carinae; dorsolateral margin of pronotal plate strongly projecting laterad; scutellar foveae shallow or indistinct; mesopleural impression present, conspicuous .... **Paraulacini**

– Female antenna filiform or slightly expanded towards apex; last flagellomere not wider than penultimate; male antenna not modified or with only F1 modified; ventral area of gena without vertical carinae; dorsolateral margin of pronotal plate not projecting laterad; scutellar foveae and mesopleural impression present or absent 2

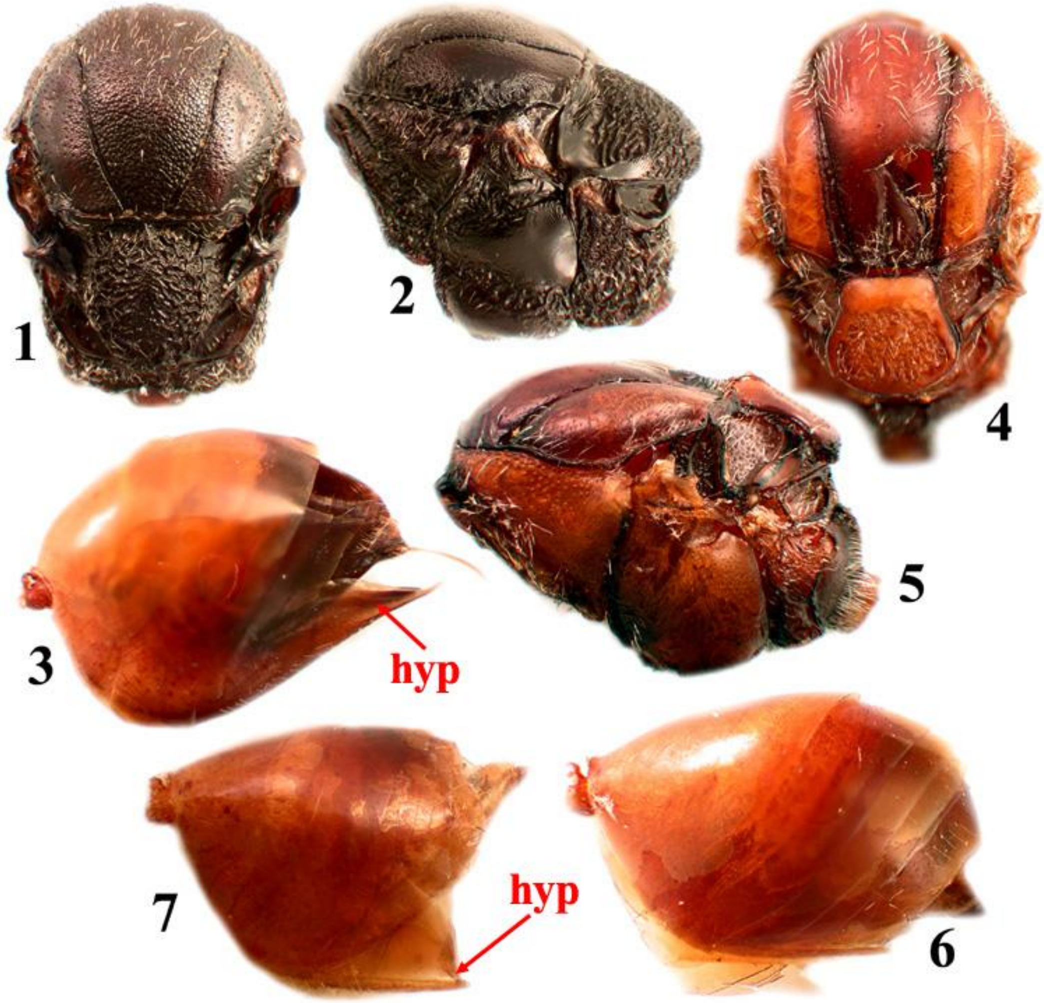
2. Frons between antennal toruli with strong longitudinal carina; notaulus and scutellar foveae absent; dorso-axillar area large, triangular and situated in same plane as mesoscutellum; Rs+M and R1 of fore wing inconspicuous, basal vein absent ….. **Eschatocerini**

– Frons between antennal toruli without strong longitudinal carina; notaulus and scutellar foveae usually present; dorso-axillar area situated in different plane compared to mesoscutellum; Rs+M and R1 of fore wing usually conspicuous, basal vein present 3

3. Scutellar foveae faint or absent (Figs 1, 4); mesopleuron with longitudinal impression (Figs 2, 5); female antenna with 12 or more flagellomeres; male F1 not modified; hypopygium ploughshaped (Figs 3, 7) or hypopygial spine short (Fig. 6) 4

– Scutellar foveae usually well differentiated, deep, sometimes confluent and forming transverse depression (Figs 8, 11, 14); mesopleuron smooth or sculptured, without longitudinal impression (Figs 9, 12, 15); female antenna usually with 10–11 flagellomeres, rarely more; male F1 usually modified; hypopygium never plough-shaped, with short or long hypopygial spine (Figs 10, 13, 16) ……………………………………………………………………………………5

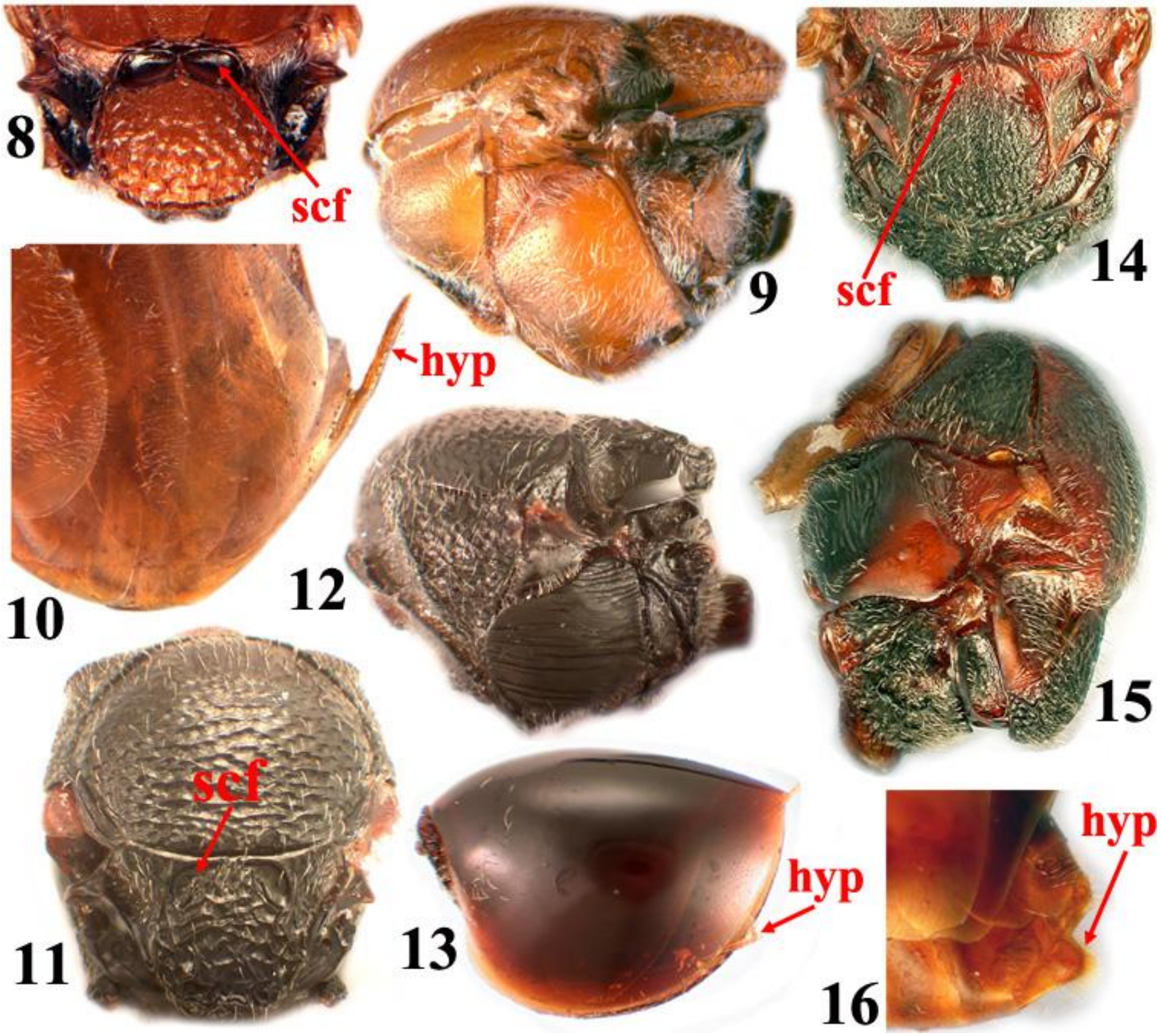
4. Pronotum short dorsomedially, admedian depressions of pronotum not visible, pronotal plate absent; mesopleural impression broad, crenulate (Fig. 2); mesoscutellum dorsally convex, without rounded impressed area (Fig. 1); lateral propodeal carinae absent (Fig. 17); hypopygium plough-shaped (Fig. 3) ………………………………………………………………………**Diplolepidini**



FIGURES 1–7. 1–3, *Diplolepis rosae*, female: 1, mesosoma, dorsal view, 2, mesosoma, lateral view, 3, metasoma, lateral view (hyp, hypopygium). 4–6, *Pediaspis aceris*, asexual female: 4, mesosoma, dorsal view, 5, mesosoma, lateral view, 6, metasoma, lateral view. 7, *Pediaspis aceris*, sexual female, metasoma, lateral view (hyp, hypopygium).

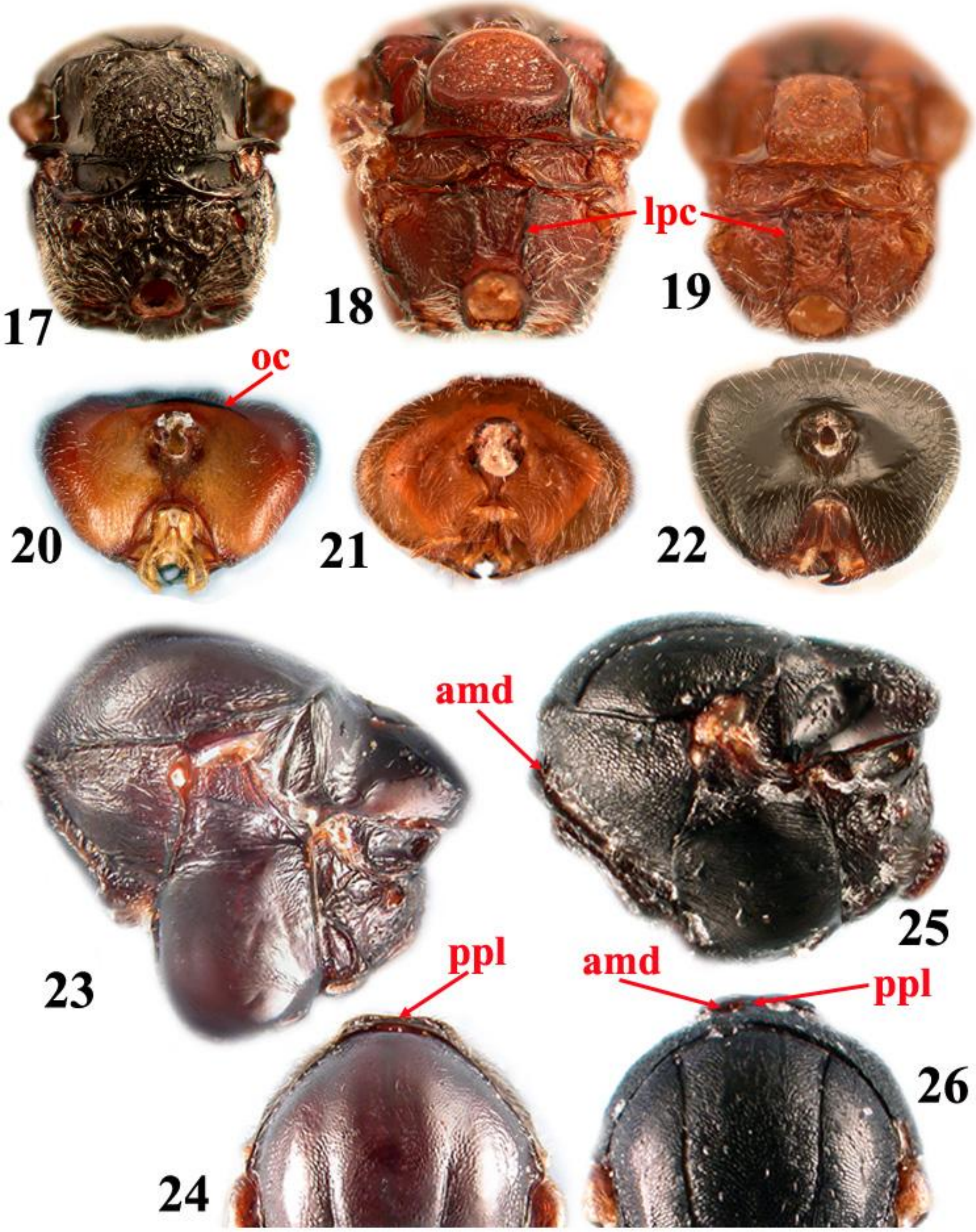
– Pronotum longer dorsomedially, admedian depressions of pronotum clearly visible and with conspicuous pronotal plate; mesopleural impression linear, narrow, without crenulate sculpture (Fig. 5); mesoscutellum dorsally flat with rounded impressed area (Fig. 4); lateral propodeal carinae present (Figs 18–19); hypopygium not plough-shaped (Figs 6–7) .... **Pediaspidini**

5\. Occiput with strong, sharp occipital carina (Fig. 20); hypopygium abrupt, not prolonged into a ventral spine; with dense tuft of long setae (Fig. 16); radial cell closed on anterior margin of fore wing ………...........…….. **Qwaqwaiini**



FIGURES 8–16. 8–10, *Andricus anatolicus*, asexual female: 8, mesoscutellum, dorsal view (scf, scutellar fovea), 9, mesosoma, lateral view, 10 metasoma, part, lateral view (hyp, hypopygium). 11–13, *Saphonecrus undulatus*, female: 11, mesosoma, dorsal view (scf, scutellar fovea), 12, mesosoma, lateral view, 13, metasoma, part, lateral view. 14–16, *Qwaqwaia scolopiae*, female: 14, mesoscutellum, dorsal view (scf, scutellar fovea), 15, mesosoma, lateral view, 16, metasoma, part, lateral view (hyp, hypopygium).

– Occiput without distinct, sharp occipital carina (Figs 21–22); hypopygium with more or less distinct, elongated, needle-like ventral spine, with subapical setae only rarely forming dense tuft (Figs 10, 13); radial cell closed or open 6

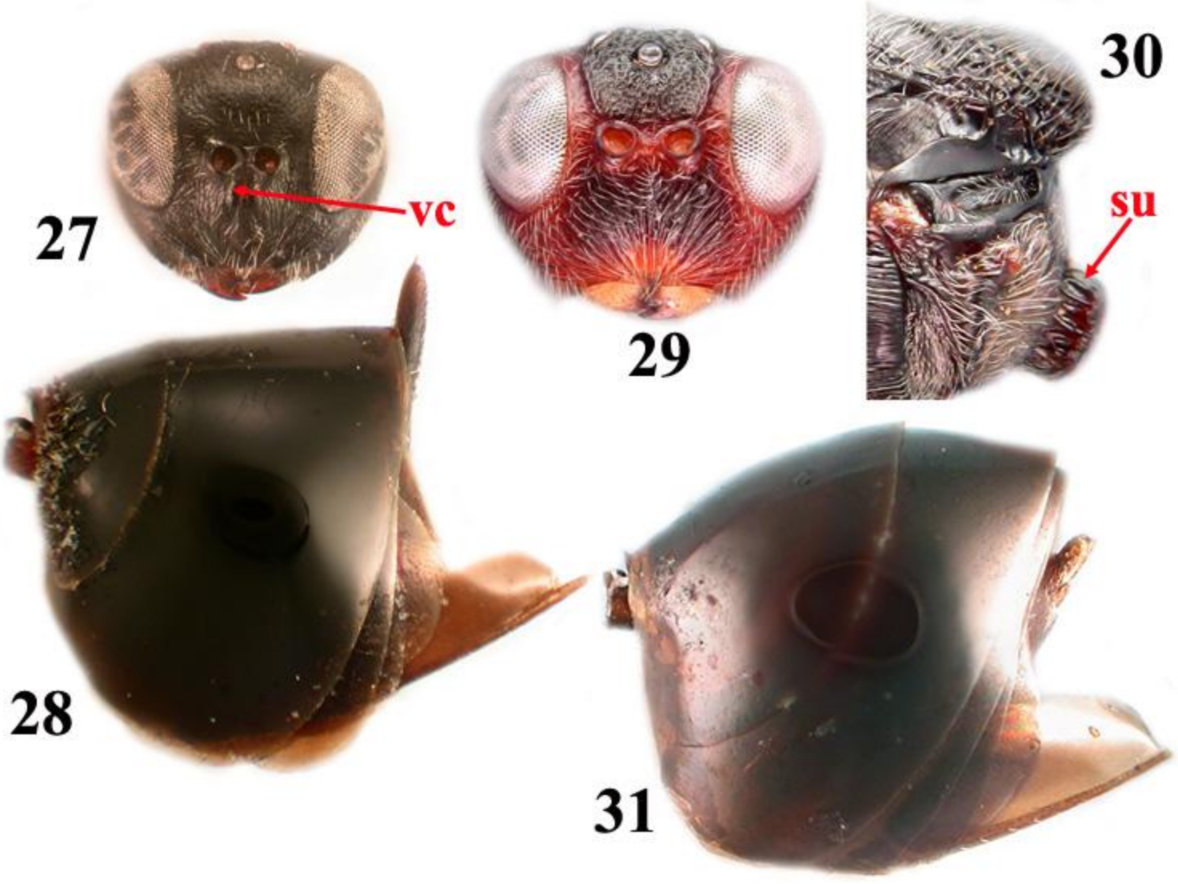


FIGURES 17–26. 17–19, propodeum, posterodorsal view: 17, *Diplolepis rosae*, female, 18, *Pediaspis aceris*, asexual female (lpc, lateral propodeal carina), 19, *Pediaspis aceris*, sexual female. 20–22, head, posterior view: 20, *Qwaqwaia scolopiae*, female (oc, occipital carina), 21, *Andricus anatolicus*, asexual female, 22, *Saphonecrus undulatus*, female. 23–24, *Neuroterus quercusbaccarum*, asexual female: 23, mesosoma, lateral view, 24, mesoscutum, part, dorsal view (ppl, pronotal plate). 25–26, *Aulacidea acroptilonica*, female: 25, mesosoma, lateral view (amd, admedian depression), 26, mesoscutum, part, dorsal view (amd, admedian depression, ppl, pronotal plate).

6. Basal part of pronotal plate small, short medially; admedian depressions of pronotum absent, or forming weak, shallow, continuous depression; pronotum dorsomedially short, 1/7 or less of length of outer lateral margin (Figs 23–24) .... **Cynipini**

– Basal part of pronotal plate usually bigger, visible; admedian depressions of pronotum usually clearly visible, more or less widely separated (Fig. 26); pronotum dorsomedially longer, 1/5 to 1/3 as long as greatest length of outer lateral margin, rarely shorter but then admedian depressions present (Figs 25–26) 7

7. Distinct raised vertical carina from ventral margin of antennal socket present, at least close to antennal socket (Fig. 27); 2nd metasomal tergite in both sexes small, free, not fused with fourth, with dense hair patch anterolaterally (Fig. 28); female antenna with 10 flagellomeres; radial cell of fore wing always closed along anterior margin ……......................………….…..... **Ceroptresini**



FIGURES 27–31. 27–28, *Ceroptres cerri*, female: 27, head, frontal view (vc, vertical carina), 28, metasoma, lateral view. 29, *Synergus formosanus*, female, head, frontal view; 30, mesosoma, posterior part, lateral view (su, longitudinal sulci on nucha), 31, *Aulacidea acroptilonica*, female, metasoma, lateral view.

– Distinct raised vertical carina from ventral margin of antennal socket absent, sometimes several weaker carinae present in this region (Fig. 29); 2nd metasomal tergite either free, but not small, or fused with fourth into one large syntergite (Figs 13, 31); anterolateral hair patch present or not; female antenna with 10–12 flagellomeres; radial cell of fore wing open or closed along anterior margin 8

8. Abdominal terga 3+4 in both sexes fused into one large syntergite, occupying nearly entire metasoma (Fig. 13); dorsal part of pronotal plate incomplete, its lateral margins marked only ventrally (Figs 11–12); head and/or mesosoma usually strongly sculptured (Fig. 29); nucha and first ring-shaped metasomal tergite with longitudinal sulci (Fig. 30)
.... **Synergini sensu stricto**

– Abdominal terga 3–8 free in most cases (Fig. 31); if terga 3+4 fused in females into one large sclerite then the corresponding terga not fused in males and pronotal plate distinct, with lateral margins marked almost entirely (Fig. 26); nucha without longitudinal sulci (Fig. 25); first metasomal tergite usually crescent-shaped and smooth (Fig. 31) .... **Aulacini sensu lato***

*includes Diastrophini (with *Periclistus* and *Synophromorpha*), Phanacidini, Aylacini sensu stricto, Aulacideini.

3.1.2. Key to Synergini sensu stricto genera

For the identification of the seven inquiline genera of Synergini, we propose the following key, which is the most updated one, including elements and new pictures which were not presented in other, earlier proposed Synergini keys (Pénzes *et al.* 2012).

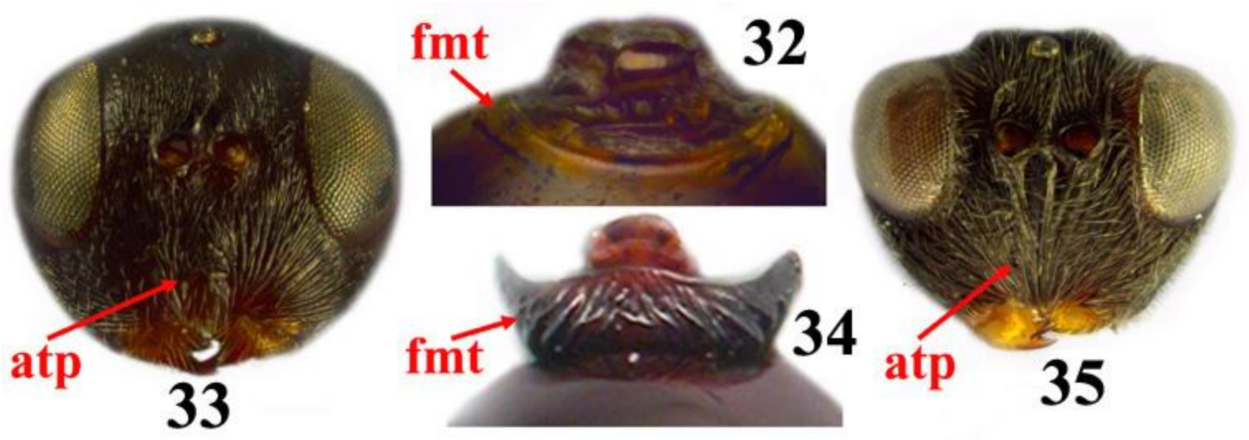
Key to Synergini sensu stricto genera

1. First metasomal tergite smooth, reduced to dorsal crescent-shaped projecting scale (Fig. 32); clypeus distinctly separated from lower face, anterior tentorial pit deep (Fig. 33) ….. ***Rhoophilus***

– First metasomal tergite in a form of ring or collar, sulcate at least laterally (Fig. 34); clypeus indistinctly separated from lower face, anterior tentorial pit indistinct (Fig. 35) …....…............ 2

2. Head trapezoid in anterior view, strongly convex ventrally (Fig. 36); 2.5–2.8x as broad as long in dorsal view; interocellar triangle narrow, posterior edge of frontal ocellus lies on a line between anterior edges of lateral ocelli (Fig. 37); anterior part of pronotum rectangular in dorsal

view, right angle between anterior and lateral sides present; 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 oriented almost at a right angle to each other; dorsomedian part of pronotum invisible in dorsal view (Figs 38–39) .... ***Ufo***



FIGURES 32–35. 32–33, *Rhoophilus loewi*, female: 32, first metasomal tergite (fmt), dorsal view, 33, head, frontal view (atp, frontal tentorial pit). 34, *Synergus kawakamii*, female, first metasomal tergite (fmt), dorsal view. 35, *Synergus belizinellus*, female, head, frontal view (atp, frontal tentorial pit).

– Head rounded or ovate in anterior view, less convex ventrally (Figs 40, 44, 48, 50); 1.6–2.1x as broad as long from dorsal view; interocellar triangle always broader, posterior edge of frontal ocellus lies away from a line between anterior edges of lateral ocelli (Figs 41, 45, 49, 51); lateral pronotal carina absent or present; right angle between anterior and lateral sides absent; dorsomedian part of pronotum visible in dorsal view (Figs 42–43, 46–47, 52–53) 3

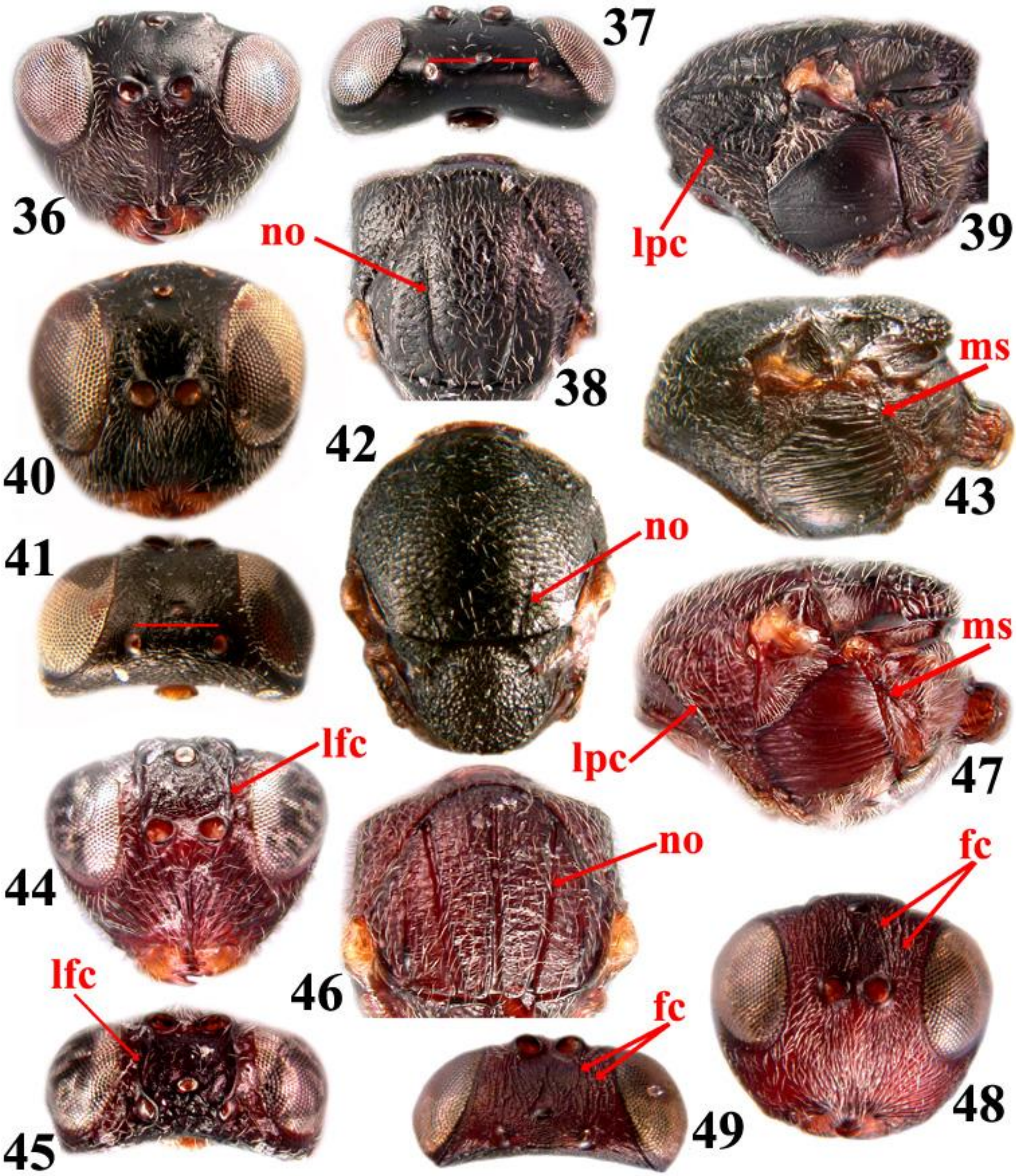
3. Pedicel 2.5x as long as scape and F2; male antenna with 11 flagellomeres .... ***Agastoroxenia***

– Pedicel shorter than scape and F2; male antenna with 12–14 flagellomeres 4

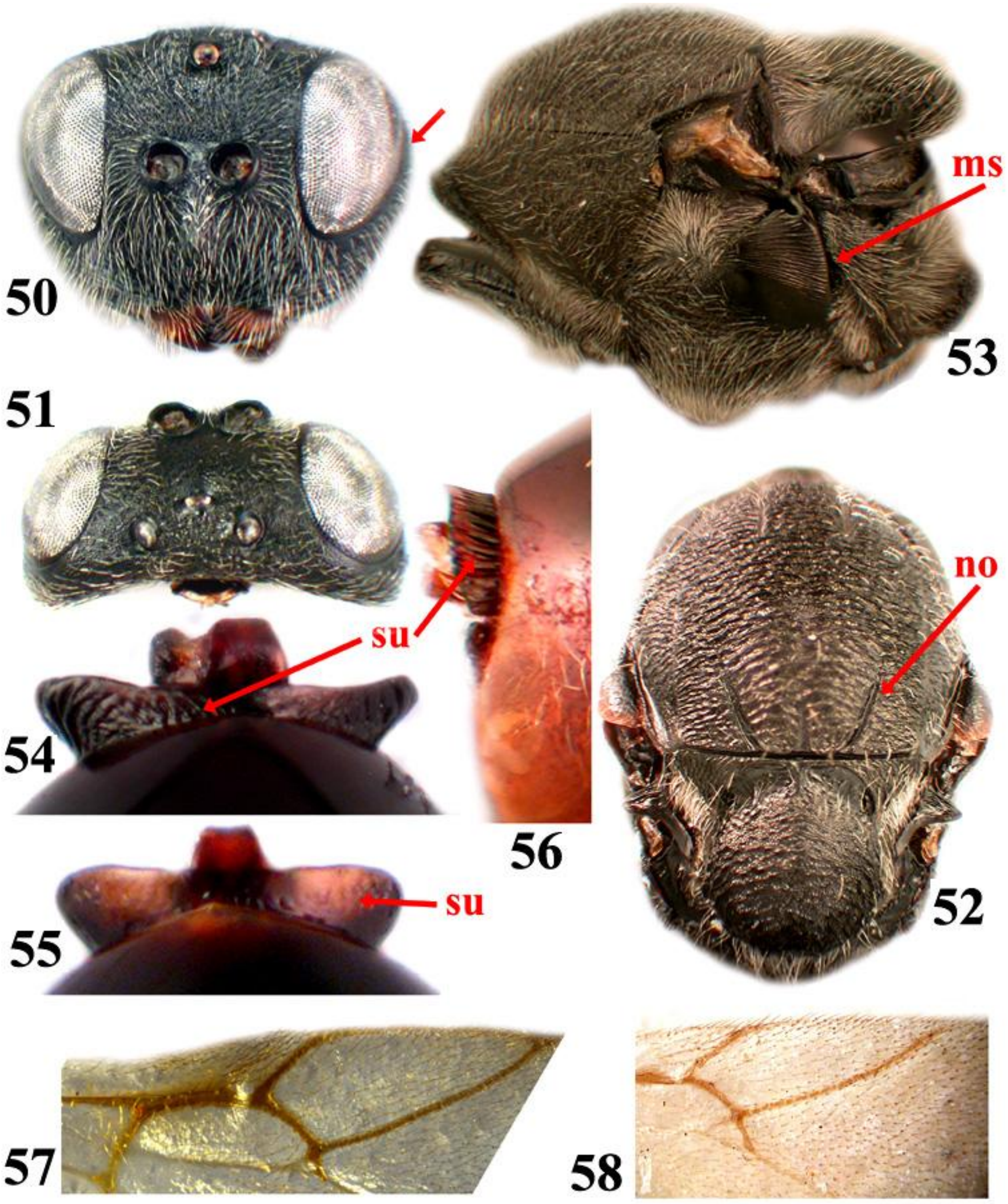
4. Lateral frontal carina present (Fig. 44); radial cell of forewing usually closed (Fig. 57), if open or partially open (in *Synergus kawakamii* and *S. castaneus*), then lateral pronotal carina present .... ***Synergus***

– Lateral frontal carina absent (Figs 48, 50); radial cell of forewing open (Fig. 58) …..........….. 5

5. Metapleural sulcus reaching posterior margin of mesopectus slightly higher than half of its height (Fig. 53); first metasomal tergite smooth medially, sulcate only laterally (Figs 54–55) .... ***Synophrus***

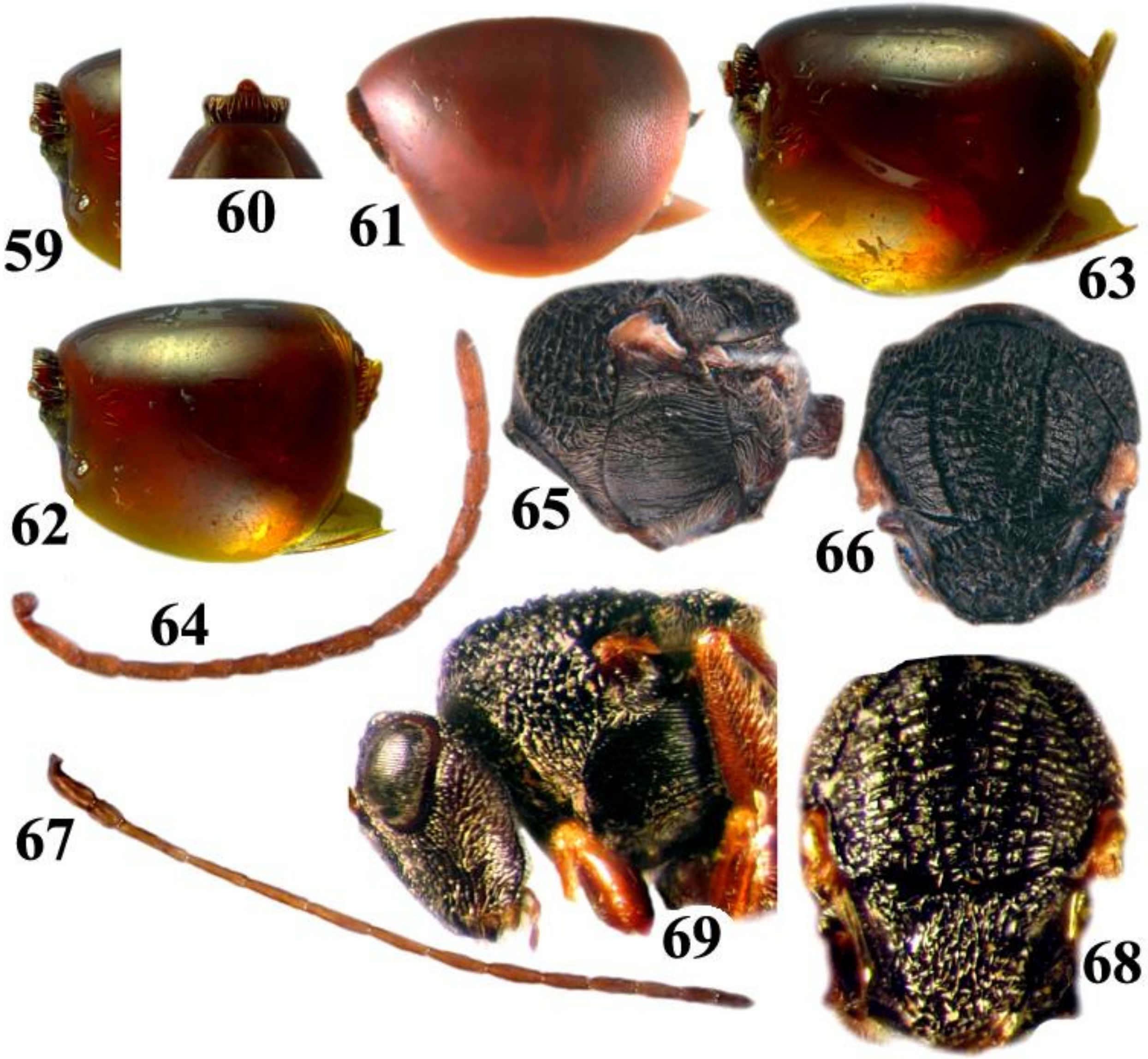


FIGURES 36–49. 36–39, *Ufo nipponicus*, female: 35–37, head: 36, frontal view, 37, dorsal view (red line indicates that laterall ocelli in one row with frontal ocellus); 38–39, mesoscutum: 38, dorsal view (no, notaulus), 39, lateral view (lpc, lateral propodeal carina). 40–43, *Saphonecrus connatus*, female: 40–41, head: 40, frontal view, 41, dorsal view; 42–43, mesoscutum: 42, dorsal view, 43, lateral view (ms, metapleural sulcus). 44–47, *Synergus xialongmeni*, female: 44–45, head: 44, frontal view (lfc, lateral frontal carina), 45, dorsal view; 46–47, mesoscutum: 46, dorsal view, 47, lateral view. 48–49, *Lithosaphonecrus huisuni*, female, head: 48, frontal view, 49, dorsal view (fc, frontal carinae).



FIGURES 50–58. 50–51, *Synophrus hungaricus*, female, head: 50, frontal view (red arrow indicates broadened gena behind eye), 51, dorsal view. 52–54, *Synophrus politus*, female: 52–53, mesoscutum: 52, dorsal view, 53, lateral view (ms, metapleural sulcus); 54, first metasomal tergite, dorsal view (su, longitudinal sulci). 55, *Synophrus pilulae*, female, first metasomal tergite, dorsal view. 56, *Synergus umbraculus*, female, first metasomal tergite, lateral view. 57–58, forewing, part, female: 57, *Synergus khazani*, 58, *Saphonecrus chaodongzhui*.

– Metapleural sulcus reaching posterior margin of mesopectus at 1/4–1/5 of its height (Fig. 43); first metasomal tergite sulcate laterally and dorsally (Figs 56, 59–60) ……..............…………... 6



FIGURES 59–69. 59–60, *Saphonecrus chinensis*, metasoma: 59, part, lateral view, 60, part, dorsal view. 61–63, metasoma, female, lateral view: 61, *Lithosaphonecrus huisuni*, 62, *Saphonecrus chinensis*, 63, *Saphonecrus robustus.* 64–66, *Lithosaphonecrus dakengi*, female: 64, antenna, 65–66, mesosoma: 65, dorsal view, 66, lateral view. 67–69, *Saphonecrus serratus*, female: 67, antenna, 68–69, mesosoma: 68, dorsal view, 69, lateral view.

6. Frons with numerous parallel rugae, extending from toruli to lateral ocelli (Figs 48–49); syntergite posteriorly punctured or reticulate, with sculptured band extending for at least to 1/4–1/5 length of syntergite and reaches ventral edge of tergite (Fig. 61) ……..….....................…........… 7

– Frons without frontal rugae, smooth, alutaceous, microreticulate, micropunctate or coriaceous (Figs 50–51); syntergite neither punctured nor reticulate, if indistinct punctures present than only as dorsoposterior patch, punctures never reaches ventral edge of tergite (Figs 62–63) ………….. ..…………………………………………………………………….......... ***Saphonecrus***

7. Female antenna with 11 flagellomeres, female F1 1.5–1.9x as long as F2 (Fig. 64); lateral pronotal carina complete, sides of pronotum sharply angled in dorsal view (Figs 65–66); body length 1.4–1.9 mm ....***Lithosaphonecrus***

– Female antenna with 12 flagellomeres, female F1 1.2x as long as F2 (Fig. 67); lateral pronotal carina partially present, weak, sides of pronotum rounded in dorsal view (Figs 68–69); body length 2.7 mm ……….............................………..................…………. ***Saphonecrus serratus****

*for easier identification and some unique characters, *S. serratus* was keyed out away from *Saphonecrus*.

Below a brief overview for the Synergini sensu stricto genera is given in alphabetical order (Pénzes *et al.* 2012, Schwéger *et al*. 2015a, b).

3.1.3. *Agastoroxenia* Nieves-Aldrey & Medianero, 2010

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 & Medianero 2010). We were unable to obtain specimens for DNA isolation, thus this genus is not represented in our phylogenetic analysis.

3.1.4. *Lithosaphonecrus* Tang, Melika & Bozsó, 2013

Only five EP *Saphonecrus* species, *S. shirakashii, S. shirokashicola, S. naiquanlini, S. yukawai*, and *S. excisus*, share the following two characters with *Lithosaphonecrus*: the female antenna with 11 flagellomeres and presence of a lateral pronotal carina. However, morphologically *Lithosaphonecrus* is a very distinct genus containing species exclusively associated with *Lithocarpus* species. A number of unique morphological characters separate the genus from all other inquiline species are as follows: rounded or very slightly trapezoid robust head with irregular interrupted frontal carinae extending from toruli to ocelli; the mesopleuron is reticuloso-striate; scutellar foveae are confluent or if median carina present then with an indistinct, glossy base with strong longitudinal parallel wrinkles; fused metasomal tergites 2+3 are posteriorly punctured or reticulate, the sculptured band extending for at least to 1/4–1/5 length of fused tergites, always reaching the ventral edge of the tergite. Moreover, in *Lithosaphonecrus* species, F1 in the female antenna 1.5–1.9x longer than F2, F11 2.0x longer than F10; F1 in male antenna 2.6–3.0x longer than F2, while in the above-mentioned *Saphonecrus* species, F1 in the female and male antennae are 1.1–1.4x longer than F2; F11 in the female antenna always nearly equal to F10 length. In the mentioned *Saphonecrus* species, the frons is always smooth or alutaceous, shiny, never with carinae as in *Lithosaphonecrus* and metasomal tergite 2+3 without punctured or reticulate posterior band; if indistinct punctures present then only in a form of an anteroposterior patch, micropunctures never reach the ventral edge of the tergite. Molecular phylogeny support that *Lithosaphonecrus* forms a distinct lineage within Synergini, was described from China and Taiwan (Bozsó *et al*. 2015, online version in 2013). *Lithonecrus* Nieves-Aldrey & Butterill, with one species (*L. papuanus* Nieves-Aldrey & Butterill), emerged from undescribed galls, collected from *Lithocarpus celebicus* (Miq.) Rehd., was described from Papua New Guinea (Nieves-Aldrey & Butterill 2014). The only diagnostic character that was given by the authors to distinguish *Lithonecrus* from *Lithosaphonecrus* is the presence of the lateral pronotal carina in *Lithonecrus* and its absence in *Lithosaphonecrus*. However, the lateral pronotal carina is present in all *Lithosaphonecrus* species, too (Bozsó *et al*. 2015, online 2013). All other characters are the same and thus, *Lithonecrus* was synonymized to *Lithosaphonecrus* (Schwéger *et al*. 2015b). Unfortunately no “Lithonecrus’’ specimens were obtained for molecular phylogenetic analysis. Thus, *Lithosaphonecrus papuanus* (Nieves-Aldrey & Butterill, 2014) has been established. Recently, a new inquiline, *Synophrus vietnamensis* Abe, Ide, Konishi & Ueno was described from Vietnam (Abe *et al*. 2014a). The examination of the detailed description and provided illustrations showed that this species errouneosly was assigned to *Synophrus* and based on all characters, it was transferred to *Lithosaphonecrus*: *Lithosaphonecrus* *vietnamensis* (Abe, Ide, Konishi & Ueno) (Schwéger *et al*. 2015b). A key to species was given in Bozsó *et al*. (2015). Currently known *Lithosaphonecrus* species are summarized in Table 4. Morphological peculiarities and host galls of *Lithosaphonecrus* are depicted in Appendix 9.1. (Figs A1–A24).

Table 4. *Lithosaphonecrus* species: distribution and host associations

***Lithosaphonecrus* species**	**Distribution**	**Host gallwasp**	**Host plant**
L. formosanus Melika & Tang, 2013	Taiwan	undescribed bud, catkin and stem galls	*Lithocarpus konishii* *L. hancei* and *L. glabra*
L. dakengi Tang & Pujade-Villar, 2013	Taiwan	bud gall	*L. hancei*
L. huisuni Tang, Bozsó & Melika, 2013	Taiwan	bud gall	*L. glabra*
L. yunnani Tang, Bozsó & Melika, 2013	China	bud gall	*L. fenestratus*
L. vietnamensis Abe, Ide, Konishi & Ueno, 2014	Vietnam	bud gall	*Castanopsis* sp.
L. papuanus Nieves-Aldrey & Butterill, 2014	Papua New Guinea	unknown gall	*L. celebicus*

3.1.5. *Rhoophilus* Mayr, 1881

Rhoophilus is morphologically related to the Holarctic inquiline genera *Synergus*, S*aphonecrus*, and *Synophrus*, all of which typically attack oak cynipid galls (van Noort *et al.* 2007). A sister group relationship between *Rhoophilus* and the oak inquiline genera *Synergus* + *Synophrus* + *Saphonecrus* was hypothesized by Ronquist (1994) and Liljeblad & Ronquist (1998). Shared diagnostic characters include the following: the ventral margin of the clypeus 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. *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 (Aethiopian) distribution (Liljeblad *et al*. 2011). *Eschatocerus* (gall inducers on *Acacia* and *Prosopis*) and *Rhoophilus* may represent the remnants of the oldest primitive lineages of cynipids (Nylander *et al*. 2004, Ronquist *et al*. 2015). Morphological peculiarities of *Rhoophilus* are depicted in Appendix 9.1. (Figs A25–A39).

3.1.6. *Synophrus* Hartig, 1843

Morphologically, *Synophrus* appears most closely related to *Saphonecrus* (Melika 2006, Pénzes *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; a male antenna has 13 flagellomeres; lateral propodeal carina is absent, the pronotum is rounded in dorsal view; the radial cell in the forewing is opened (Pénzes *et al*. 2009). Currently 7 *Synophrus* species are known, all from the Western Palearctic only (Table 5) and all of which are able to impose their own gall phenotypes on those of their hosts (Pénzes *et al*. 2009). 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 further 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 inquilines, and attack by *Synophrus* is always lethal to the host gallwasp. *Synophrus* is known from section Cerris of genus *Quercus* exclusively. Morphological peculiarities and modified galls of *Synophrus* are depicted in Appendix 9.1. (Figs A40–A48).

Table 5. *Synophrus* species: distribution and host associations

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

3.1.7. *Ufo* Melika & Pujade, 2005

Ufo was described from Japan with one species, *U. abei* Melika & Pujade-Villar (Melika *et al*. 2005). Later, *U. koreanus* Melika, Pujade-Villar & Choi was described from Republic of Korea (Melika *et al*. 2007). Both species are inquilines in oak galls on *Quercus* subgenus *Quercus* section Cerris (Fagaceae). All *Ufo* species are known only from EP, synapomomorphies and generic diagnostic characters of which were discussed in details earlier (Melika *et al*. 2005, 2007). *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 Synergini sensu stricto. Comparing to *Synergus* and *Saphonecrus, Ufo* possesses with a few synapomorphies: the head is trapezoid in frontal 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. Based on these characters *Ufo* forms a distinct group within Synergini. Two species, *U. shirakashii* (Shinji) and *U. shirokashicola* (Shinji), were described from Japan from cynipid galls associated with *Quercus* subgenus *Cyclobalanopsis* (Wachi *et al*. 2011b) and later were transferred to *Saphonecrus* (Melika *et al*. 2012). Currently 4 *Ufo* species are known from the EP: *U. abei* Melika & Pujade-Villar, 2005, *U. koreanus* Melika, Pujade-Villar & Choi, 2007, *U. cerroneuroteri* Tang & Melika, 2012, *U. nipponicus* Melika, 2012. All these species are known to associate with oak gallwasps developing in section Cerris of genus *Quercus* oaks (Melika *et al*. 2012). Molecular phylogeny suggests that it is a sister taxon of a recently described *Saphonecrus* lineage (Pénzes *et al.* 2012, Bozsó *et al*. 2014, Schwéger *et al.* 2015b). Morphological peculiarities and host galls of *Ufo* are depicted in Appendix 9.1. (Figs A49–A70).

3.2. *Saphonecrus* Dalla Torre, 1910

3.2.1. General comments

Saphonecrus closely resembles *Synergus* (Pénzes *et al*. 2009, Ács *et al*. 2010, Melika *et al*. 2012, Schwéger *et al*. 2015a, b). The two genera can be separated by a combination of characters:

Saphonecrus species have an open radial cell in the fore wing, the female antenna usually with 11 flagellomeres, and the lateral frontal carina absent. In contrast, most *Synergus* species have a closed radial cell, the female antenna with 12 flagellomeres and complete or partially complete lateral frontal carina always present (Pujade-Villar & Nieves-Aldrey 1990, Melika *et al.* 2006). Morphological peculiarities and host galls of *Saphonecrus* are depicted in Appendix 9.1. (Figs A71–A100). However, in *Synergus* there are exceptions from these character states, *Synergus castaneus*, *S. plagiotrochi*, and the recently described *Synergus kawakamii* Tang & Melika from Taiwan (Schwéger *et al*. 2015b), are species with open or partially open radial cell of the fore wing. In these species, the female antenna with 12 flagellomeres, the notaulus is complete, reaching the anterior margin of the mesocutum, complete or incomplete lateral frontal carina present. Only one consistent morphological character is found to distinguish *Saphonecrus* from *Synergus*: the presence (*Synergus*) or absence (*Saphonecrus*) of the lateral frontal carina. The separation of this genus from *Synergus* has subsequently been widely questioned (Eady & Quinlan 1963, Ritchie 1984, Pujade-Villar & Nieves-Aldrey 1990), and 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 & Nieves-Aldrey (1990) revised the European species and maintained the genus, but also questioned its validity. We consider *Saphonecrus* not to be monophyletic and closely allied to *Synergus* (Pénzes *et al*. 2012, Bozsó *et al*. 2014, 2015, Schwéger *et al*. 2015a, b).

To this point 24 species of *Saphonecrus* were known worldwide (Pénzes *et al*. 2012, Bozsó *et al*. 2014). The WP species are associated mainly with galls on section Cerris of genus *Quercus* oaks, while some are associated with galls that develop on white oaks (section Quercus). The species generally have a single generation per year and emerge after overwintering in the gall, but those on evergreen oaks have at least the potential for two generations per year (Pujade-Villar & Nieves-Aldrey 1990). The European species can be divided into three groups on the basis of their biology: (i) species with one annual generation, and associated with galls on section Quercus oaks (*S. connatus* (Hartig)); (ii) also univoltine species, associated with galls on section Cerris oaks (*S. undulatus* (Mayr), *S. haimi* (Mayr), and *S. irani* Melika & Pujade-Villar); (iii) two Mediterranean species, with bivoltine life cycles, associated with galls on evergreen oaks of section Cerris (*S. barbotini* Pujade-Villar & Nieves-

Aldrey and *S. gallaepomiformis* (Boyer de Fonscolombe)) (Pujade-Villar & Nieves-Aldrey 1990).

Four *Saphonecrus* species were listed for the Nearctic (Burks 1979) and some of them possess some non-typical character states for *Saphonecrus*, and their assignment to *Saphonecrus* must be examined in detail. In 2007, seven *Saphonecrus* species were listed for the Eastern Palearctic (Abe *et al*. 2007) and two species, *S. serratus* Weld and *S. areolatus* Weld, were known from the Oriental Region (Weld 1926). Also new species were described from Japan and China (Liu *et al.* 2012, Wang *et al.* 2010, Wachi *et al.* 2011b, Pujade-Villar *et al*. 2014) and recently we described 15 new species from Japan, Russia, China and Taiwan: *Saphonecrus chinensis* Tang & Schwéger, *S. gilvus* Melika & Schwéger, S. *globosus* Schwéger & Tang, *S. leleyi* Melika & Schwéger, *S. lithocarpii* Schwéger & Melika, *S. longinuxi* Schwéger & Melika, *S. morii* Schwéger & Tang, *S. nantoui* Tang, Schwéger & Melika, *S. nichollsi* Schwéger & Melika, *S. pachylomai* Schwéger, Tang & Melika, *S. robustus* Schwéger & Melika, *S. saliciniai* Melika, Tang & Schwéger, *S. shanzhukui* Melika & Tang, *S. symbioticus* Melika & Schwéger, and *S. taitungi* Schwéger, Tang & Melika. The taxonomic assignment, data on biology and distribution for all known *Saphonecrus* species are given below; morphological descriptions and diagnoses are given in Schwéger *et al*. (2015a). Thus, currently 36 valid species of *Saphonecrus* are known worldwide (Table 6).

Preliminary molecular phylogenetic analysis suggests many clades within *Saphonecrus*, three of them include EP and WP Paleartic *Saphonecrus* species, too (Pénzes *et al*. 2012, Bozsó *et al*. 2014). All of the newly described EP *Saphonecrus* species (Schwéger *et al*. 2015b) are characterized distinct *coxI* haplotypes (“barcodes”), which support the delimitation of novel species established by the morphology. However, molecular phylogeny does not support some of morphological groups of species and *Saphonecrus* does not appear to be monophyletic (Bozsó *et al*. 2014, see also section Results 3.4.).

Table 6. *Saphonecrus* species: world distribution and host associations (after Schwéger *et al*. 2015a)

Species	**Distribution***	**Host plants**
S. areolatus Weld, 1926	O: Philippines, Luzon	Unknown
S. barbotini Pujade-Villar & Nieves-Aldrey, 1985	WP: Iberia	*Quercus* sect. Cerris
S. brevicornis (Ashmead, 1896)	NA: California	Unknown
S. chaodongzhui Melika, Ács & Bechtold, 2004	EP: China, Yunnan	Unknown
S. chinensis Tang & Schwéger, 2015	EP: China	*Lithocarpus*
S. connatus (Hartig, 1840)	WP: Europe	*Quercus* sect. Quercus
S. diversus Belizin, 1968	EP: Far East Russia	Unknown
S. excisus (Kieffer, 1904)	EP: Bengal, Kurseong	*Lithocarpus*
S. favanus Weld, 1944	NA: DC and Missouri	*Quercus* sect. Lobatae
S. flavitibilis Wang & Chen, 2010	EP: China, Zhejiang	Unknown
S. gallaepomiformis (Boyer de Fonsc., 1832)	WP: Iberia	*Quercus* sect. Cerris
S. gemmariae Ashmead, 1885	NA: USA, Florida	*Quercus* sect. Lobatae
S. gilvus Melika & Schwéger, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. globosus Schwéger & Tang, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. haimi (Mayr, 1872)	WP: Europe, N.Africa	*Quercus* sect. Cerris
S. irani Melika & Pujade-Villar, 2006	WP: Iran	*Quercus* sect. Cerris
S. leleyi Melika & Schwéger, 2015	EP: Russia, Far East	*Quercus* sect. Quercus
S. lithocarpii Schwéger & Melika, 2015	EP: Taiwan	*Lithocarpus*
S. longinuxi Schwéger & Melika, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. morii Schwéger & Tang, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. naiquanlini Melika, Ács & Bechtold, 2004	EP: China, Zhejiang	Unknown
S. nantoui Tang, Schwéger & Melika, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. nichollsi Schwéger & Melika, 2015	EP: Taiwan	*Lithocarpus*
S. pachylomai Schwéger, Tang & Melika, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. reticulatus Pujade-Villar, Wang & Guo, 2014	EP: China	*Quercus* sect. Quercus
S. robustus Schwéger & Melika, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. serratus Weld, 1926	O: Philippines, Luzon	Unknown
S. saliciniai Melika, Tang & Schwéger, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. shanzhukui Melika & Tang, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. shirakashii (Shinji, 1940)	EP: Japan, Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. shirokashicola (Shinji, 1941)	EP: Japan, Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. sinicus Belizin, 1968	EP: China, Sichuan	Unknown
S. symbioticus Melika & Schwéger, 2015	EP: Russia, Japan	*Quercus* sect. Quercus
S. taitungi Schwéger, Tang & Melika, 2015	EP: Taiwan	*Quercus* subgenus *Cyclobalanopsis*
S. tianmushanus Wang & Chen, 2010	EP: China, Zhejiang	Unknown
S. undulatus (Mayr, 1872)	WP: Europe	*Quercus* sect. Cerris
Total species number: 36 species		

* O – Oriental region, WP, EP, Western and Eastern Palearctic, NA – Nearctic

3.2.2. Key to the Palearctic *Saphonecrus* species

For the identification of all Palearctic *Saphonecrus* species for the first time a species-complete key is proposed (Schwéger *et al.* 2015b).

Key to Palearctic *Saphonecrus* Dalla Torre & Kieffer species

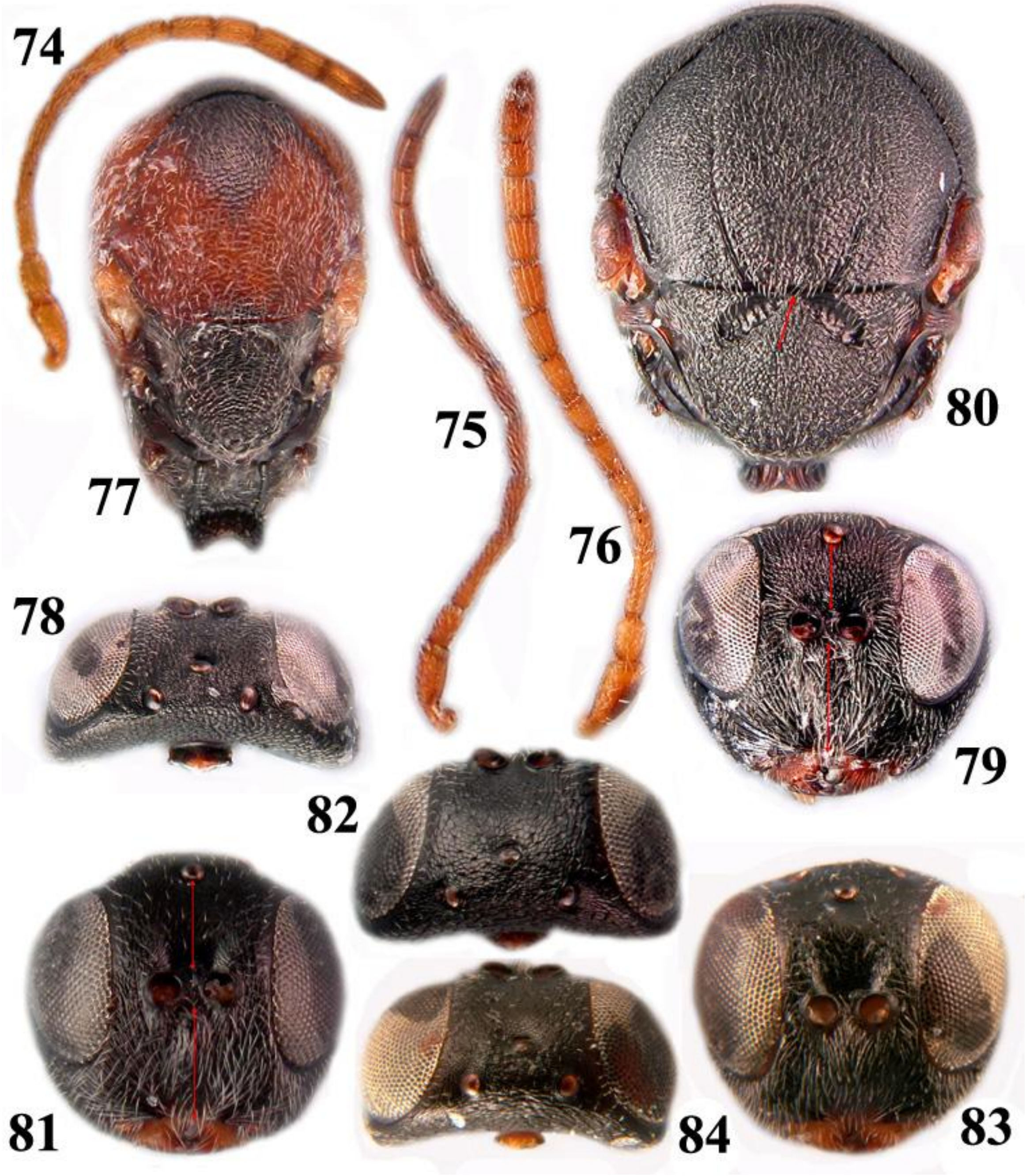
1. Base of mesoscutellum nearly as broad as mesoscutum posteriorly; dorsoaxillar area narrow, inconspicuous; syntergite without row of setae anterolaterally ……............................... ***S. sinicus***

– Base of mesoscutellum narrower than posterior width of mesoscutum, dorsoaxillar area distinct and broad; syntergite with row of short white setae anterolaterally 2

FIGURES 70–73. 70–71, *Saphonecrus chaodongzhui*, mesosoma, female: 70, lateral view, 71, dorsal view. 72–73, *S. naiquanlini*, mesosoma, female: 72, lateral view, 73, dorsal view.

2. Lateral pronotal carina absent, anterolateral sides of pronotum rounded in dorsal view (Figs 70–71) ……………………………..................………………………………………………………... 3

– Lateral pronotal carina present, complete or partially complete, anterolateral sides of pronotum usually sharply angled in dorsal view (Figs 72–73) ……......................………………………….…… 11



FIGURES 74–84. 74–76, antenna, female: 74, *S. barbotini*, 75, *S. gallaepomiformis*, 76, *S. chaodongzhui*. 77, *S. gallaepomiformis*, female, mesosoma, dorsal view. 78–79, *S. symbioticus*, female: 78, head, frontal view, 79, head, dorsal view, 80, mesosoma, dorsal view. 81–82, *S. leleyi*, female, head: 81, frontal view, 82, dorsal view. 83–84, *S. chaodongzhui*, female, head: 83, frontal view, 84, dorsal view.

3. Radial cell of fore wing less than 2.0x as long as broad ………............................… ***S. irani****

– Radial cell more than 2.5x as long as broad ……………………….......…………....…… 4

4. Head, mesosoma and metasoma brown, if black than only partially ……….......…...……… 5

– Head and mesosoma black, metasoma black or dark brown ……..….....……........…..…….. 7

5. Female F1 equal F2 and F3 (Fig. 74) ……………………..…………….......….. ***S. barbotini***

– Female F1 about 2.0x as long as F2 (Figs 75–76) …………………….....………………..… 6

6. Mesoscutum uniformly dark brown to black, with distinct transverse interrupted rugae, with smooth interspaces between rugae; notaulus extending at least to half length of mesoscutum (Fig. 71) ………………………………….………………..............…..……….. ***S. chaodongzhui***

– Mesoscutum reddish brown with black area only between anterior parallel lines, delicately coriaceous, without transverse interrupted rugae; notaulus present in posterior 1/4 of mesoscutum length (in some specimens absent) (Fig. 77.)......................….…***S. gallaepomiformis***

7. Female antenna with 12 flagellomeres, female F1 slightly broadened apically; notaulus complete, extending to anterior margin of mesoscutum, anterior parallel line extending to 1/5 of mesoscutum length ………………………...........……………….…..……..… ***S. tianmushanus***

– Female antenna with 11 flagellomeres, female F1 not broadened apically; notaulus incomplete, extending to 1/3–2/3 of mesoscutum length, impressed only in posterior half, gradually narrowing till anterior end of mesoscutum; anterior parallel line absent ……......…… 8

8. Female F1 1.6–2.0x as long as F2; antenna, tibiae, tarsi pale yellow …......…...… ***S. flavitibilis***

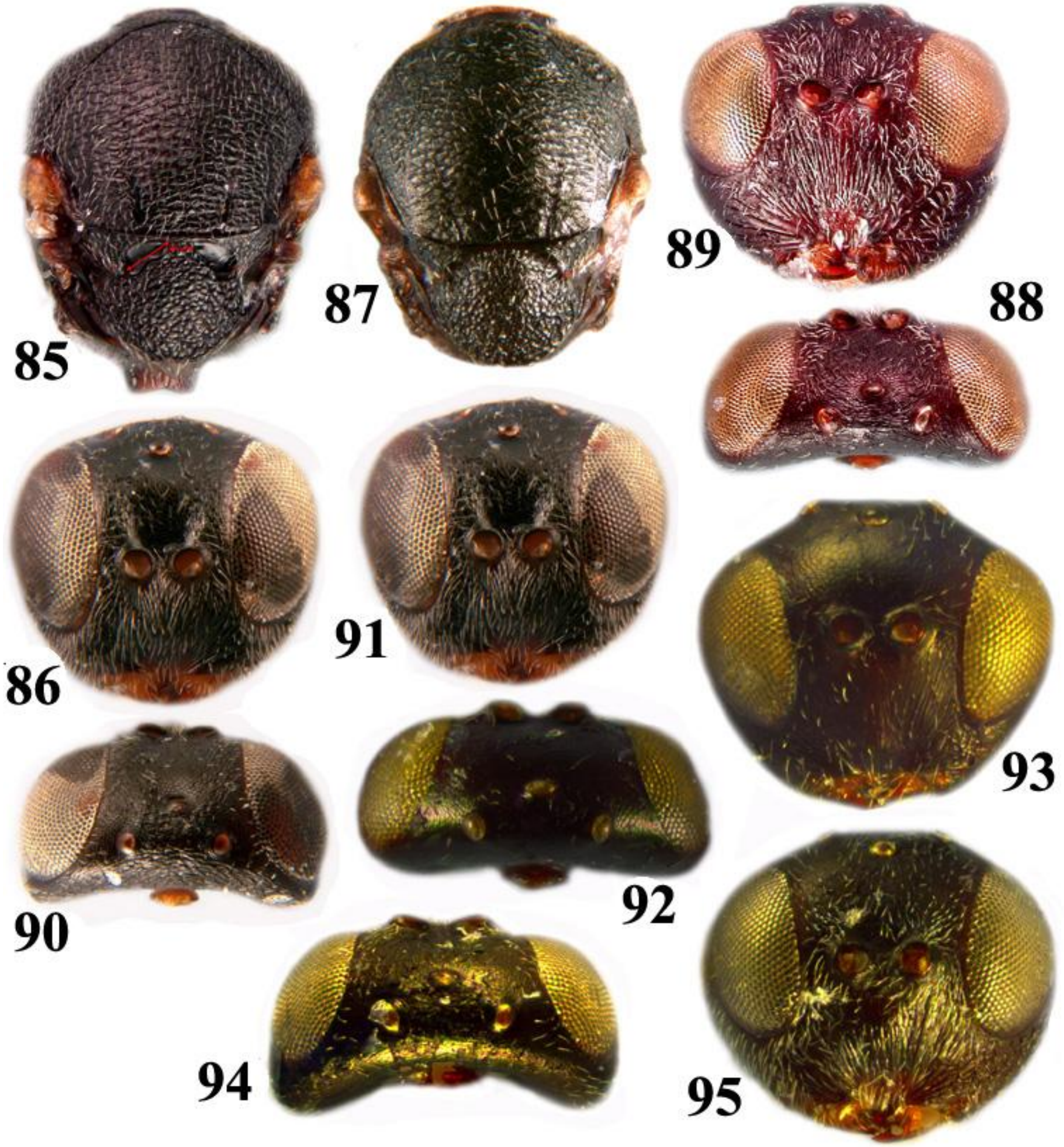
– Female F1 1.1–1.3x as long as F2; antenna, tibiae, tarsi brown …………....….…………..… 9

9. Head in dorsal view 2.1x as broad as long (Fig. 78); torulus slightly above mid height of eye, lower face 1.6x as high as height of frons (Fig. 79); notaulus complete (Fig. 80) ………………………………………………………….....………..………… ***S. symbioticus***

– Head in dorsal view 1.6–1.8x as broad as long (Figs 82, 84); torulus in lower half of eye height, lower face 1.2x as high as height of frons (Figs 81, 83); notaulus incomplete (Fig. 85) ………………………………………………………......……………..…..……..………… 10

10. Frons with deep punctures (Figs 81–82); notaulus extending to 2/3 of mesoscutum length, gradually narrowing till anterior margin of mesoscutum (Fig. 85); scutellar foveae kidney-shaped, with smooth bottom, posteriorly well-delimited from disk of mesoscutellum; median

area between foveae broad, fovea 2.0x as long as width of median area (Fig. 85); males unknown .... ***S. leleyi***



FIGURES 85–95. 85, *S. leleyi*, female, mesosoma, dorsal view. 86–87, *S. connatus*, female: 86, head, frontal view, 87, mesosoma, dorsal view. 88–89, *S. naiquanlini*, female, head: 88, dorsal view, 89, frontal view. 90–91, *S. chinensis*, female, head: 90, dorsal view, 91, frontal view. 92–93, *S. globosus*, female, head: 92, dorsal view, 93, frontal view. 94–95, *S. taitungi*, female, head: 94, dorsal view, 95, frontal view.

– Frons without punctures (Fig. 86); notaulus extending to 1/3–1/4 of mesoscutum length (Fig. 87); scutellar foveae ovate, with coriaceous bottom, posteriorly indistinctly delimited from disk; median area between foveae narrow, triangulate (Fig. 87); males known ………..…. ***S. connatus***

11. Radial cell of fore wing less than 2.0x as long as broad ……….......………………. ***S. irani***

– Radial cell more than 2.5x as long as broad ……………………………………..………....... 12

12. Notaulus uniformly impressed, complete, reaching anterior margin of mesoscutum …....... 13

– Notaulus anteriorly less impressed than posteriorly, incomplete or absent, if incomplete than extending to half of mesoscutum length ………………..……………………………………… 29

13. Mesopectus with longitudinal striae not extending to anterior margin of mesopectus, reticulate in anterior part and between striae ……………………..........………. ***S. reticulatus***

– Mesopectus with longitudinal striae extending to anterior margin of mesopectus, area between striae smooth or delicately coriaceous ………………………..……..................…………... 14

14. Mesoscutum with strong and long transverse rugae, especially between notauli; body length more than 2.5 mm …………………………................…………..……………………… 15

– Mesoscutum coriaceous, without or with delicate and short rugae; body length 1.3–2.0 mm ……………………………………………………………………...…………......………. 17

15. Head reddish brown, mesoscutum black or reddish brown; female F1 longer than F2; male known ……………………………………………………….……………………....…....….. 16

– Head and mesoscutum black; female F1=F2; male unknown ………......……..…. ***S. areolatus***

16. POL 2.3x as long as OOL (Fig. 88); male known …………….......…………. ***S. naiquanlini***

– POL 1.25x as long as OOL; male unknown ……………………....……... ***S. hupingshanensis***

17. Gena smooth, glabrous; scutellar foveae narrow, transversely ovate; lateral propodeal carina curved outwards anteriorly... ***S. diversus***

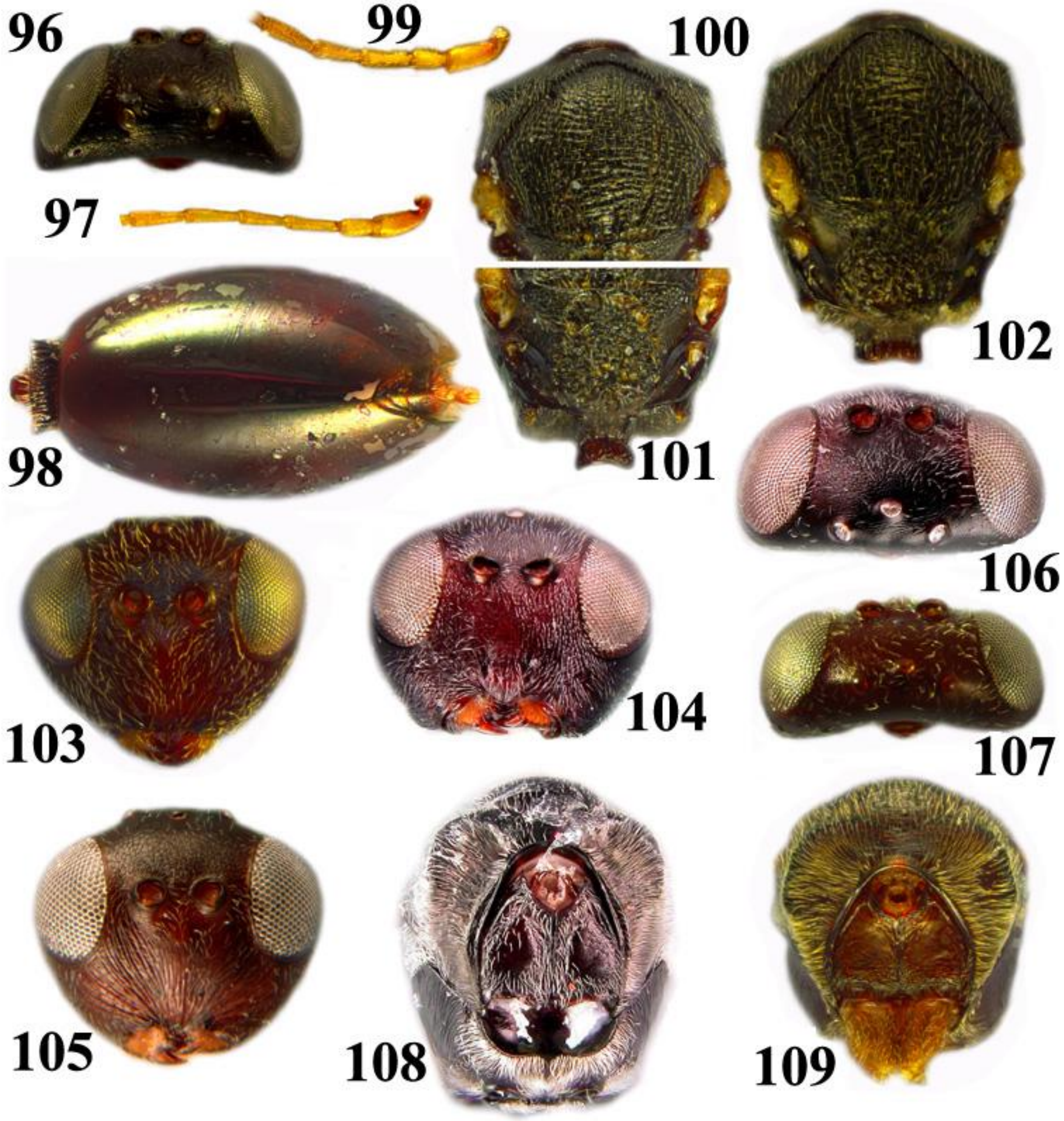
– Gena alutaceous, matt; scutellar foveae as broad as high or higher than broad; lateral propodeal carinae parallel 18

18. Frons and interocellar area with delicate transverse striae (Figs 88–89) .... ***S. naiquanlini***

– Frons and interocellar area smooth, alutaceous or coriaceous, without transverse striae (Figs 90–91, 92–93) 19

19. Gena broadened behind eye, visible in frontal and dorsal views (Figs 90–91, 94–95) 20

– Gena not broadened behind eye, invisible in frontal and dorsal views (Figs 92–93) …........... 22



FIGURES 96–109. 96–98, *S. robustus*, female: 96, head dorsal view, 97, antenna, part, 98, metasoma, dorsal view. 99–101, *S. chinensis*, female: 99, antenna, part, 100, mesoscutum, dorsal view, 101, mesoscutellum, dorsal view. 102, *S. taitungi*, female, mesosoma, dorsal view. 103–105, head, frontal view: 103, *S. morii*, 104, *S. nantoui*, 105, *S. gilvus*. 106–107, head, dorsal view, female: 106, *S. nantoui*, 107, *S. morii*. 108–109, pronotum and propleuron, frontal view, female: 108, *S. nantoui*, 109, *S. morii*.

20. Scutellar foveae rounded; POL 2.7x as long as OOL (Fig. 96); female F1 1.2x as long as F2 (Fig. 97); female syntergite dorsoposteriorly incised; prominent part of ventral spine of hypopygium 2.5x as long as broad in ventral view (Fig. 98); male unknown …....… ***S. robustus***

– Scutellar foveae transverse or kidney-shaped, obliquely orientated backwards; POL 1.9–2.2x as long as OOL (Fig. 90); female F1 equal or only slightly longer than F2 (Fig. 99); female syntergite dorsoposteriorly not or very slightly incised; prominent part of ventral spine of hypopygium as long as broad in ventral view; male known ……….............…………...…… 21

21. Anterior notaular pit deep, bottom of notaulus with rugae (Fig. 100); scutellar foveae transverse (Fig. 101) …………………………………………………...….......…… ***S. chinensis***

– Anterior notaular pit absent, bottom of notaulus smooth, without rugae (Fig. 102); scutellar foveae kidney-shaped, orientated obliquely backwards (Fig. 102) …........…………... ***S. taitungi***

22. Malar space and lower face without or with indistinct delicate striae laterally, mid part of lower face without striae (Figs 90, 103) 23

– Malar space and lower face with striae reaching torulus and extending into space between eye and torulus (Fig. 105) …………………………………….………..........................…… 24

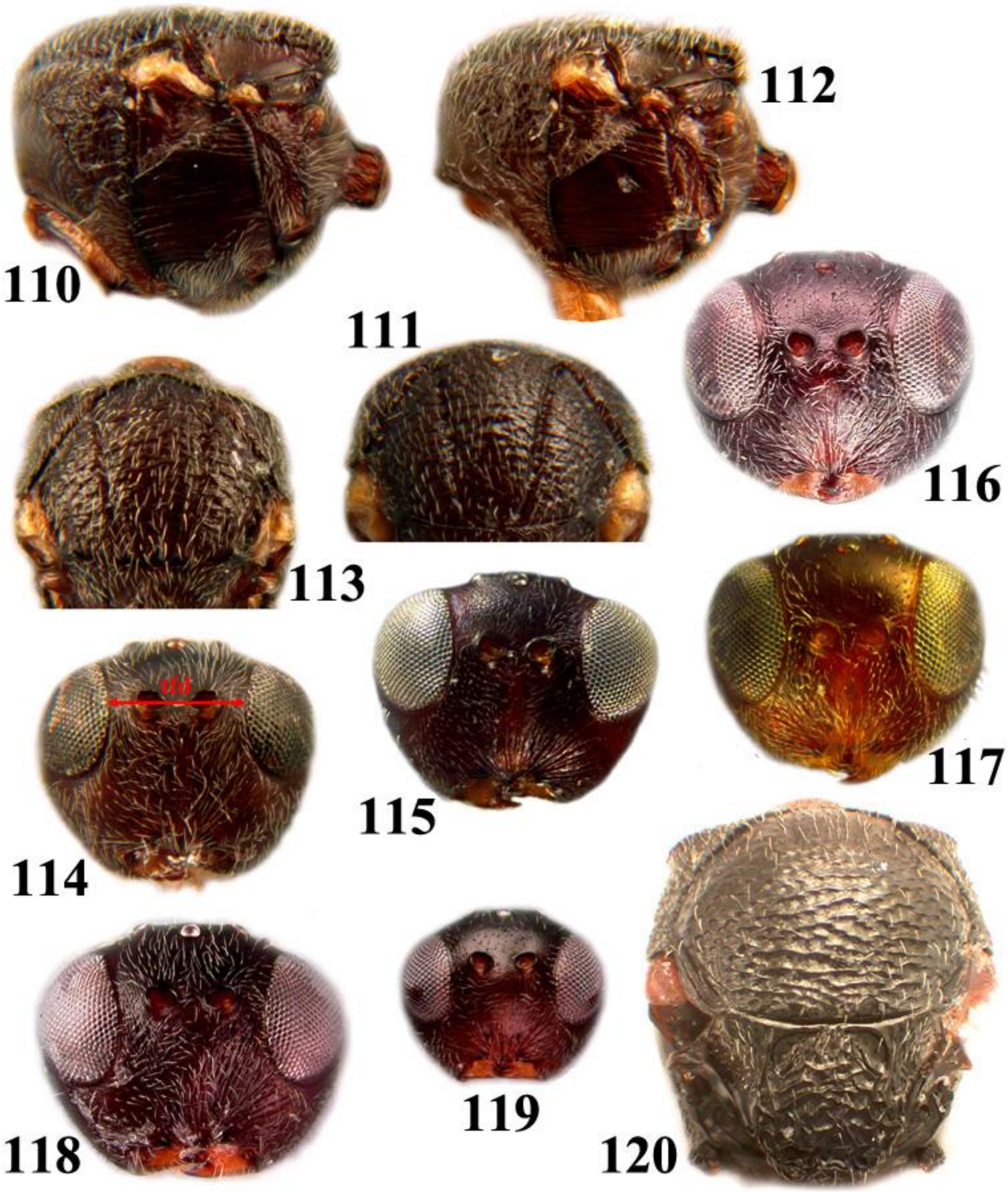
23. Head quadrangular in frontal view, eye 1.6x as high as length of malar space (Fig. 104); POL 2.0x as long as OOL (Fig. 106); propleuron with dense setae laterally (Fig. 108); scutellar foveae rounded, nearly as high as broad; male F1 1.2x as long as F2, slightly broadened apically and basally …………………………………….……………….....……… ***S. nantoui***

– Head trapezoid in frontal view, eye 0.7x as high as length of malar space (Fig. 103); POL 2.5x as long as OOL (Fig. 107); propleuron without dense setae laterally (Fig. 109); scutellar foveae transverse, broader than high; male F1 1.2x as long as F2, slightly broadened apically, not broadened basally ………………………………………………………….…… ***S. morii***

24. Pronotum rounded dorsolaterally, not sharply angled, pronotal carina short (Figs 110–111); transfacial distance 1.2x as long as height of eye (Fig. 105); female F1 1.7x as long as F2, F11 2.5x as long as F10; male F1 2.3x as long as F2 …………………..........................…. ***S. gilvus***

– Pronotum sharply angled dorsolaterally, pronotal carina complete (Figs 112–113); transfacial distance equal or slightly longer than height of eye (Figs 114–115); female F1 1.2–1.4x as long as F2, F11 2.0x as long as F10; male F1 1.2–1.7x as long as F2 ……….........................…… 25

25. Eye 1.2–1.3x as high as length of malar space (Figs 114–115); female F1 about 1.5x as long as F2 ……..……………………………………………………..….. 26



FIGURES 110–120. 110–111, *S. gilvus*, female: 110, mesosoma, lateral view, 111, mesoscutum, dorsal view. 112–113, *S. pachylomai*, female: 112, mesosoma, lateral view, 113, mesoscutum, dorsal view. 114–117, female, head, frontal view: 114, *S. pachylomai*, 115, *S. shanzhukui*. 116, *S. lithocarpii*, 117, *S. nichollsi*. 118–119, *S. shirakashii*, head, frontal view: 118, female, 119, male. 120, *S. undulatus*, female, mesosoma, dorsal view.

– Eye 1.6–2.0x as high as length of malar space (Fig. 117); female F1 less than 1.5x as long as F2 ………………………………………………………........…………………….……….. 27

26. Transfacial distance equal to height of eye (Fig. 115); radial cell 3.0x as long as broad; metasoma in female as high as long in lateral view, syntergite dorsoposteriorly slightly incised …………………………………………………………………...............…… ***S. shanzhukui***

– Transfacial distance longer than height of eye (Fig. 114); radial cell 3.9x as long as broad; metasoma in female 1.2x as long as high in lateral view, syntergite dorso-posteriorly not incised; male F1 curved in mid height, not broadened basally ……….....................……… ***S. pachylomai***

27. Transfacial distance shorter than height of eye; lower face uniformly setose, frons with setae only laterally, along eye, central part of frons with sparse scattered setae (Figs 116–117); male head with denser setae than in female; male F1 1.2x as long as F2, broadened only apically; female metasoma not incised dorsoposteriorly …………………........................…………. 28

– Transfacial distance longer than height of eye; lower face and frons with uniform dense setae; male head with sparse whitish setae like in female (Figs 118–119); male F1 1.6–1.8x as long as F2, slightly broadened apically and basally; female metasoma slightly incised dorsoposteriorly ……………………………………………….................................………… ***S. shirakashii***

28. Head trapezoid, 1.3× as broad as high in frontal view (Fig. 116); scutellar foveae ovate, as broad as long; radial cell 2.7x as long as broad; female pedicel 1.7x as long as broad; male F1 slightly longer than F2, F3=F4 ……………………………………...................…… ***S. lithocarpii***

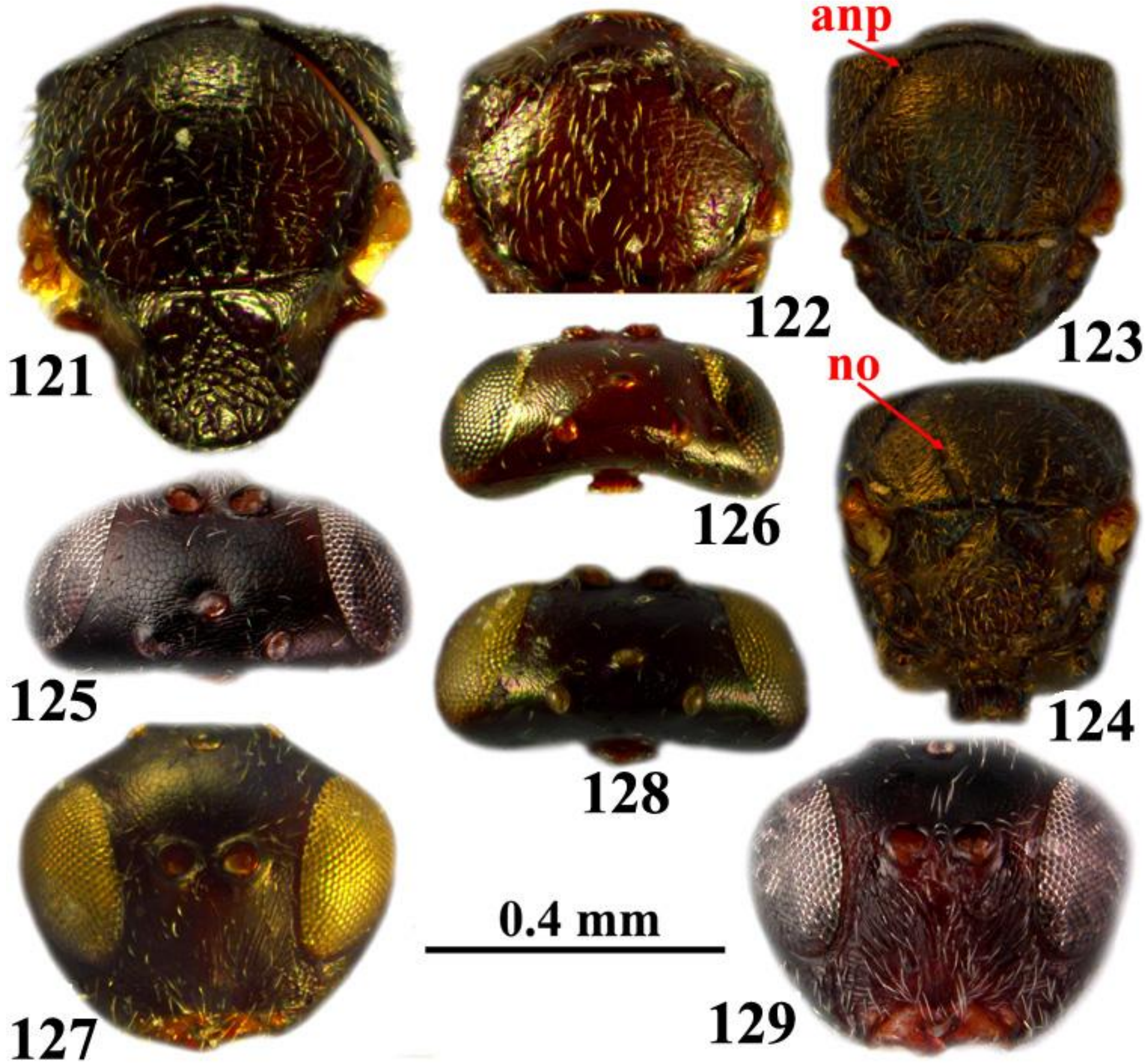
– Head rounded, as broad as high in frontal view (Fig. 117); scutellar foveae transverse, longer than broad, obliquelly orientated backwards to disk of mesoscutellum; radial cell 3.4x as long as broad; female pedicel 3.0x as long as broad; male F1=F2, F4 shorter than F3 ……………………………………………………….......………..…………..…… ***S. nichollsi***

29. Notauli absent (Fig. 120) ………………………………...……………………………..…. 30

– Notauli incomplete, extending to half of mesoscutum length, anteriorly less impressed than posteriorly (Figs 121–122, 123–124) ………………………….…….…………………...… 31

30. Mesoscutum with strong elevated interrupted transverse rugae, area between rugae smooth, broader than width of ruga (Fig. 120); mesoscutellum with strong irregular rugae (Fig. 120) …………………………………………………………………………….……………. ***S. undulatus***

– Mesoscutum without transverse rugae, coriaceous; mesoscutellum delicately coriaceous, without rugae ……………………………..…………..……………….….………… ***S. haimi***



FIGURES 121–129. 121, *S. globosus*, female, mesosoma, dorsal view, 122, *S. longinuxi*, female, mesoscutum, dorsal view. 123–124, *S. saliciniai*, female, mesosoma: 123, dorsal view (anp, frontal notaulur pit), 124, posterodorsal view (no, notaulus). 125–126, head, dorsal view, female: 125, S. *shirokashicola*, 126, *S. longinuxi*. 127–128, *S. globosus*, head, female: 127, frontal view, 128, dorsal view. 129, *S. shirokashicola*, female, head, frontal view.

31. Anterior notaular pit absent; antenna and legs whitish; western palearctic …..........… ***S. haimi***

– Anterior notaular pit present (Figs 121–122), antenna and legs brown; eastern palearctic ……………………………………………………………………….…….………...……..…...….... 32

32. POL 1.9–2.3x as long as OOL (Figs 110–111, 125); female F1 1.7–2.0x as long as F2 33

– POL 2.9x as long as OOL (Fig. 126); female F1 1.3x as long or equal to F2 ……....…….. 34

33. Head and mesosoma black to dark brown, metasoma dark brown, dorsally darker; POL 2.3× as long as OOL (Fig. 128); transfacial distance as long as height of eye (Fig. 127) ………………………………………………………………………..…..…...…… ***S. globosus***

– Head and mesosoma reddish brown, metasoma lighter; POL 1.9x as long as OOL (Fig. 125), transfacial distance longer than height of eye (Fig. 129) …….................…….. ***S. shirokashicola***

34. Head and mesosoma black to dark brown; female pedicel 2.1x as long as broad, F1 1.3x as long as F2, F11 2.1× as long as F10; male F1 1.7x as long as F2 …………………… ***S. saliciniai***

– Head and mesosoma reddish brown; female pedicel subglobose, F1 nearly equal to F2, F11 1.7× as long as F10; male F1 slightly longer than F2 ……………………………..… ***S. longinuxi***

(**S. irani* is keyed out twice, with and without lateral propodeal carina; in some specimens lateral pronotal carina distinct, while in others absent or indistinct).

3.2.3. Annotated list of worldwide *Saphonecrus* species

Below we gave a worldwide *Saphonecrus* species list with some data on their biology, distribution, morphological peculiarities (Schwéger *et al.* 2015b). Species are listed in alphabetical order.

Saphonecrus areolatus Weld, 1926

A detail description of the species was given by Weld (1926). The female holotype, deposited at the United States National Museum (USNM), was examined. This species possesses the following unique morphological characters: the gena is broadened behind the eye, visible in frontal view behind the eye; the female antenna with 12 flagellomeres, F1=F2; the mesoscutum has strong and long transverse rugae, especially between the complete notauli, which reach the anterior margin of the mesoscutum; the metanotal trough has dense white setae; the lateral propodeal carinae are not parallel, slightly curved outwards in the mid height of the propodeum; tarsal claws are simple, without basal lobe; syntergite strongly incised dorsally, with a band of micropunctures extending onto lateral sides of the syntergite, and dorsally to 1/6 of the syntergite length; the prominent part of the ventral spine of the hypopygium as long as broad, with a sparse long setae extending far beyond the apex of the spine. Known from Philippines (Luzon Island), host galls and host plant associations are unknown (Weld 1926).

Saphonecrus barbotini Pujade-Villar & Nieves-Aldrey, 1985 and ***Saphonecrus gallaepomiformis*** (Boyer de Fonscolombe, 1832)

Both species form a distinct lineage (Ács *et al.* 2010, see also section Results 3.4.) and associate with Mediterranean evergreen oak species (*Q. ilex*, *Q. suber*, *Q. coccifera*), with two generations per year. They attack *Plagiotrochus* galls only, especially woody galls of *P. britaniae* Barbotin and *P. coriaceus* (Mayr) in twigs (Pujade-Villar & Nieves-Aldrey 1990). Earlier, in all relevant literature, *S. gallaepomiformis* 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 followed (Pénzes *et al.* 2012).

Saphonecrus brevicornis (Ashmead, 1896)

Originally described as *Synergus* (Ashmead 1896). Weld (1952) transferred the species to *Saphonecrus* based on one character: open radial cell of the fore wing. We were unable to examine the type of *S. brevicornis*, thus cannot decide whether it is a *Saphonecrus* or a *Synergus* species with a partially open radial cell of the fore wing. Type must be examined to make a final decision, thus we leave it in *Saphonecrus* for now.

Saphonecrus chaodongzhui Melika, Ács & Bechtold, 2004

In the original description of this species the presence of weak lateral frontal carina was erroneously indicated (Melika *et al*. 2004) which, in fact, is absent. Host cynipid galls and host plant associations are unknown. Known from China, (Yunnan, Diqing, Xiaozhongdian), later was found also in Zhejiang Province of China (Wang *et al*. 2010).

Saphonecrus chinensis Tang & Schwéger, 2015

This species was reared from unknown round bud galls, flattened on top, up to 15 mm in diameter, with small depression in top surface at centre of the gall; the gall is green when fresh, turning brown when matures (Fig. A85 in Appendix 9.1.); collected from *Lithocarpus fenestratus*. Adults emerged under laboratory conditions during late April. Currently known only from China (Lan Cang County). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus connatus (Hartig, 1840)

Saphonecrus connatus is thought to be a trans-Palearctic species and was mentioned from 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). The most peculiar character of *S. connatus* is the absence of notaulus. This species attacks some *Andricus* species and galls of *Callirhytis glandium* (Giraud), *Cynips quercusfolii* (L.), *Neuroterus anthracinus* (Curtis) and *N. quercusbaccarum* (L.) (Pénzes *et al.* 2009, Pujade-Villar & Nieves-Aldrey 1990, Pujade-Villar *et al*. 2003).

Saphonecrus diversus Belizin, 1968

Based on the original description it is a *Saphonecrus* (Belizin 1968). The species was described on the basis of three females. According to Belizin (1968) most closely resembles *S. undulatus*. Known from the Far East of Russia, host galls and host plant associations are unknown (Belizin 1968). We were unable to obtain the type of this species, thus it is still need a detailed examination.

Saphonecrus excisus (Kieffer, 1904)

Based on the description (Dalla Torre & Kieffer 1910) it is a *Saphonecrus*. We tried for several years to locate the type of the species unsuccessfully and the type might be well lost. The species is known from Kurseong, West Bengal, India, reared from stem swelling-like galls of *Neuroterus haasi* Kieffer, collected from *Lithocarpus elegans*. Based on the host plant association, it is possible that this species belongs to a supposed *Saphonecrus* clade which associates exclusively with *Lithocarpus* (Bozsó *et al.* 2014, section Results 3.4.).

Saphonecrus favanus Weld, 1944

This species is known from the U.S.A. (Washington DC and Missouri), reared from a root gall of *Dryocosmus favus* Beutenmüller on section Lobatae of genus *Quercus* (red oaks) (Weld 1944). The type female was examined by us. Morphologically it is not a typical *Saphonecrus*: the frons, vertex and mesoscutum have numerous deep punctures (resembling *Synergus subterraneus*

Giraud); the head is quadrangular in the frontal view, the clypeus is impressed, the lower face is delicately coriaceous, without radiating striae; the female antenna has 11 flagellomeres; the lateral frontal and lateral pronotal carina are absent; the fore wing margin lacks cilia; the metapleural sulcus reaches the posterior margin of the mesopectus in the upper 1/3 of its height; the first metasomal tergite has parallel sulci laterally and dorsally; the last metasomal tergite has a posterodorsal patch of micropunctures. *Saphonecrus favanus* might represent a distinct, undescribed genus. More specimens and further examination are in need.

Saphonecrus flavitibilis Wang & Chen, 2010
Known from China (Zhejiang), host galls and host plant associations are unknown (Wang *et al.* 2010).

Saphonecrus gemmariae Ashmead, 1885
The species was described from Florida, based on one male, which emerged from *Callirhytis quercusgemmariae* (Ashmead) gall on red oaks (Ashmead 1885). The type supposed to be deposited at the USNM, however, was neither located in the collection by the curator, M. Buffington nor by G. Melika. The description of the male is very brief, not enough detail to make a decision whether *S. gemmariae* is a *Saphonecrus* or a *Synergus*.

Saphonecrus gilvus Melika & Schwéger, 2015
This species was reared from undescribed hairy round galls on leaf midribs (Fig. A86) on *Q. gilva.* Galls were collected in November from which adults emerged under laboratory conditions during November. Currently it is known only from Taiwan (Taichung County). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus globosus Schwéger & Tang, 2015
This species was reared from undescribed leaf galls (Fig. A87) on *Q. globosa* in May. Adults emerged under laboratory conditions in May. Currently known only from Taiwan (Nantou County). Diagnosis and detail species descriptions are given in Schwéger *et al.* (2015b).

Three species, ***Saphonecrus haimi*** (Mayr, 1872), ***Saphonecrus irani*** Melika & Pujade-Villar, 2006, ***Saphonecrus undulatus*** (Mayr, 1872), which 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), all of which are associating with *Quercus* section Cerris only.

Saphonecrus leleyi Melika & Schwéger, 2015

Wasps emerged from undescribed bud galls (Fig. A97) on *Q. mongolica* in late September and also from the asexual galls of *Andricus mukaigawae* (Pujade-Villar *et al.* 2016). Known from Far East of Russia and China (Pujade-Villar *et al.* 2016). Diagnosis and detailed species description are given in Schwéger *et al.* (2015b).

Saphonecrus lithocarpii Schwéger & Melika, 2015

This species was reared from undescribed bud galls (Fig. A87) on *Lithocarpus glabra* and leaf galls (Fig. A88) on *L. konishii.* Galls were collected in late autumn and beginning of January from which adults emerged under laboratory conditions from January till April. Currently it is known only from Taiwan (Taichung City, Nantou County). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus longinuxi Schwéger & Melika, 2015

This species was reared from undescribed small round galls on the upper surface of the leaves (Fig. A87) of *Q. longinux* in early March, from which adults emerged by the end of April. Currently it is known only from Taiwan (Nantou County). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus morii Schwéger & Tang, 2015

This species was reared from leaf galls (Fig. A91) on *Q. morii* in February and later in May. Adults emerged immediately after they were put onto laboratory rearing. Currently known only from Taiwan (Nantou County). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus naiquanlini Melika, Ács & Bechtold, 2004

Originally described from China (Zhejiang), the host cynipid gallwasp species and host plants are unknown (Melika *et al*. 2004). Later, it was collected in Yunnan Province of China (Wang *et al*. 2010).

Saphonecrus nantoui Tang, Schwéger & Melika, 2015

This species was reared from undescribed leaf petiole thickening galls (Fig. A92) on *Quercus glauca* (Thunb.) Oerst. Galls were collected in late February from which adults emerged under laboratory conditions at the beginning of March. Currently known only from Taiwan (Nantou County). Diagnosis and detailed species description are given in Schwéger *et al.* (2015b).

Saphonecrus nichollsi Schwéger & Melika, 2015

This species was reared from undescribed stem swelling-like galls (Fig. A93) on *L. konishii* in October, from which adults emerged immedeately after the galls were put onto laboratory rearing. Currently known only from Taiwan (Taichung City). Diagnosis and detailed species description are given in Schwéger *et al.* (2015b).

Saphonecrus pachylomai Schwéger, Tang & Melika, 2015

This species was reared from undescribed stem swelling-like galls (Fig. A95) on *Q. pachyloma* in late October. Adults emerged under laboratory conditions in November. Currently known only from Taiwan (Nantou County). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus reticulatus Pujade-Villar, Wang & Guo, 2014

This species was reared from rounded stem swelling galls on *Q. aliena* var. *acutiserrata* (*Quercus* section Quercus of genus *Quercus*). Inquilines emerged immediately after the galls were collected in late June in China (Zhejiang Province) (Pujade-Villar *et al*. 2014a). One unique character differentiates this species from all other *Saphonecrus* species: the reticulate anterior part of the mesopectus and the reticulate surface between longitudinal striae on the mesopectus (Pujade-Villar *et al*. 2014a).

Saphonecrus robustus Schwéger & Melika, 2015

This species was reared from undescribed *Dryocosmus* multilocular stem swelling-like galls (Fig. A100) on *Q. hypophaea* in January-March. Adults emerged immedeately after they were put in laboratory rearing. Currently known only from Taiwan (Taitung County). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus saliciniai Melika, Tang & Schwéger, 2015

This species was reared from small egg-shaped galls on leaf midribs (Fig. A99) on *Q. salicinia* in mid-February. Adults emerged under laboratory conditions by the end of March. Currently known only from Taiwan (Taipei vicinity). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus serratus Weld, 1926

The type was examined. The next characters differentiate this species from all other *Saphonecrus* species: the head is transverse in dorsal view, the female antenna has 12 flagellomeres, the female F1 is 1.2x as long as F2; the lateral pronotal carina is weak and incomplete, the sides of the pronotum are rounded in dorsal view, the mesoscutum has strong transverse rugae, the tarsal claws are simple and without basal lobe; the propodeal carinae curve outwards and are not parallel; the first metasomal tergite is not straight as in other *Saphonecrus* species but sinuate, the sulci are parallel, longitudinal, present dorsally and laterally; the syntergite has a posterodorsal patch of micropunctures; the prominent part of the ventral spine of the hypopygium is at least 2.0x as long as broad in ventral view; body length 2.7 mm. Known from Philippines (Luzon Island), host galls and host plant associations are unknown (Weld 1926).

Saphonecrus shanzhukui Melika & Tang, 2015

This species was reared from rounded stem swelling-like galls (Fig. A96) on *Q. hypophaea.* Galls were collected in January-March from which adults emerged under laboratory from January till March. Currently is known only from Taiwan (Taitung County). Diagnosis and detail species description are given in Schwéger *et al*. (2015b).

Saphonecrus shirakashii (Shinji, 1940) and ***Saphonecrus shirokashicola*** (Shinji, 1941). These two species, originally described in *Andricus* Hartig, were erroneously placed in *Ufo* (Wachi *et al*. 2011b) but were later transferred to *Saphonecrus* (Melika *et al*. 2012). *Saphonecrus shirakashii* and *S. shirokashicola* are known from Japan and Taiwan, were reared from undescribed leaf galls on *Q. glauca*, *Q. globosa* and *Q. longinux* (*Quercus* subgenus *Cyclobalanopsis*) (Melika *et al*. 2012). Both species are characterized by having an ovate or quadrangular head in frontal view; the frons is smooth or alutaceous, without or with some delicate indistinct striae; the male F1 is 1.5× as long as F2, or only slightly longer than F2; the mesoscutum is alutaceous to delicately coriaceous, without distinct short irregular transverse striae. In *S. shirakashii*, the pedicel is 2.2× as long as broad; the female F1 is 1.2× as long as F2; F11 is 1.9× as long as F10; the notaulus is complete, reaching the anterior margin of the mesoscutum, while in *S. shirokashicola*, the pedicel is 1.6× as long as broad; the female F1 is 1.7× as long as F2; F11 is 2.3× as long as F10; the notaulus is incomplete, present only in the posterior 1/3–1/2 of the mesoscutum. Molecular phylogeny suggests that the two species belong to different clades within Synergini (Bozsó *et al*. 2014, section Results 3.4.).

Saphonecrus sinicus Belizin, 1968

Based on the original description, this species is a *Saphonecrus* (Belizin 1968). The species was originally described on the basis of one female. According to Belizin (1968), this species differs from all other known *Saphonecrus* by the broad mesoscutellum, the width of which is equal to the width of the mesoscutum. The species was described from China (Sichuan); host galls and host plant associations are unknown (Belizin 1968). We were unable to locate and to obtain the type of this species, thus it is still need a detail examination.

Saphonecrus symbioticus Melika & Schwéger, 2015

All wasps emerged exclusively from the asexual galls of *Andricus hakonensis* (=*A.symbioticus*) (Fig. A98) on *Q. dentata* and *Q. mongolica* in late September-October. Currently known only from Russia (Far East, Primorskij Kraj) and Japan (Hokkaido). Diagnosis and detailed species description are given in Schwéger *et al.* (2015b).

Saphonecrus taitungi Schwéger, Tang & Melika, 2015

This species was reared from galls, collected from *L. dodoniifolius* at the beginning of March, from which adults emerged under laboratory conditions by the end of March. Currently known only from Taiwan (Taitung County). Diagnosis and detail species description are given in Schwéger *et al.* (2015b).

Saphonecrus tianmushanus Wang & Chen, 2010

The female of this species has an antenna with 12 flagellomeres, the suture between F12 and F11 is distinct. Described from China (Zhejiang), host galls and host plants are unknown (Wang *et al*. 2010).

3.3. Synergus Hartig, 1840

3.3.1. General comments

Synergus is the most species-rich inquilines genus of oak gall cynipid, with 118 known species world-wide (Table 2), with a long and complex history of taxonomic revision (see Pujade-Villar *et al*. 2003, Melika 2006). Currently 19 *Synergus* species are known from the EP including eight species recently described from Far East Russia, Japan, China and Taiwan (Sadeghi *et al*. 2006, Bernardo *et al*. 2013, Abe *et al*. 2011, Pujade-Villar *et al*. 2014, Schwéger *et al*. 2015a; Table 7). In the last decade, two *Synergus* species were described from the EP for which the host plant associations are other than *Quercus* subgenus *Quercus*. One *Synergus* species, *S. itoensis* Abe, Ide & Wachi, appeared to induce its own gall in the seed coat of the acorn of *Quercus* (subgen. *Cyclobalanopsis*) *glauca,* a unique behaviour for inquilines when the species have not lost the capability to induce its own gall (Abe *et al*. 2011). *Synergus castaneus* Pujade-Villar, Bernardo & Viggiani, described from China, is the first known cynipid inquiline (Synergini) that emerge from *Castanea* galls (Fagaceae) (but not from the well-known gall of *Dryocosmus kuriphilus* Yasumatsu) (Bernardo *et al*. 2013). A new species, *Synergus kawakamii*, is the first *Synergus* known to associate with galls developing on a *Castanopsis* species (Fagaceae) (Schwéger *et al.* 2015a). Recently, *Synergus jezoensis* Uchida & Sakagami was revised and validated (Pujade-Villar *et al*. 2014); however, the status of four other EP species described in the first half of 20th century (*S. atamiensis* Ashmead, *S. hakonensis* Ashmead, *S. iwatensis* Shinji, and *S. mizunarae* Shinji) were still uncertain (Abe *et al*. 2007). Partially it was resolved in Schwéger *et al.* (2015a).

Table 7. Eastern Palearctic *Synergus* species with distribution and host associations (after Schwéger *et al*. 2015a)

Species	Distribution	Host gall	Host plant
S. abei Melika & Schwéger	Japan	unknown acorn and bud galls	*Quercus* (subgen. *Quercus*)
S. belizinellus Schwéger & Melika	Russia Japan	*Belizinella vicina* and unknown leaf galls	*Quercus* (subgen. *Quercus*)
S. castaneus Pujade-Villar, Bernardo & Viggiani	China	unknown galls	*Castanea*
S. changtitangi Melika & Schwéger	Taiwan	unknown stem swellin-like galls	*Quercus* (subgen. *Quercus*)
S. chinensis Melika, Ács & Bechtold	China, S.Korea Russia	unknown acorn, bud and leaf galls	*Quercus* (subgen. *Quercus*)
S. deqingensis Pujade-Villar,Wang & Chen	China	Unknown	unknown
S. formosanus Schwéger & Melika	Taiwan	*Trichagalma formosana*	*Quercus* (subgen. *Quercus*)
S.gifuensis Ashmead	Japan Russia	*Andricus kashiwaphilus*, *A. mukaigawae*	*Quercus* (subgen. *Quercus*)
S. hakonensis Ashmead	Japan	Unknown	unknown
S. ishikarii Melika & Schwéger	Japan	*Ussuraspis* sp., unknown leaf galls	*Quercus* (subgen. *Quercus*)
S. itoensis Abe, Ide & Wachi	Japan	gallinducer in acorns	*Quercus* (subgen. *Cyclobalanopsis*)
S. iwatensis Shinji	status uncertain, **nomen nudum**		
S. japonicus Walker	Japan China Russia	*Andricus kashiwaphilus*, *A. mukaigawae*	*Quercus* (subgen. *Quercus*)
S. jezoensis Uchida & Sakagami	Japan China	Unknown	unknown
S. kawakamii Tang & Melika	Taiwan	unknown detachable stem galls	*Castanopsis*
S. khazani Melika & Schwéger	Russia Japan	*Andricus kashiwaphilus*, *A. mukaigawae*; unknown acorn and bud galls	*Quercus* (subgen. *Quercus*)
S. mizunarae Shinji	status uncertain, **nomen nudum**		
S. symbioticus Schwéger & Melika	Russia Japan	*Andricus hakonensis*, *A. kashiwaphilus*	*Quercus* (subgen. *Quercus*)
S. xialongmeni Melika, Ács & Bechtold	China	unknown acorn, leaf and bud galls	*Quercus* (subgen. *Quercus*)
Total: 17 valid species and 2 with uncertain status			

The presence/absence of the lateral frontal carinae and/or lateral pronotal carina, open or closed radial cell of the fore wing, and 11 or 12 flagellomeres in female antennae in *Saphonecrus*

(*Synergus*) are inconsistent character states, which in some cases make precise morphology based generic/specific identification uncertain and, thus, the establishment of unique set of character state for definition (at a generic level) is complicated. Morphological peculiarities and host galls of *Synergus* are depicted in Appendix 9.1. (Figs A101–A127). All of the newly described EP *Synergus* species described by us are supported by distinct *cox1* haplotypes supporting the morphology-based delimitation of species (Schwéger *et al*. 2015a).

3.3.2. Key to Eastern Palearctic *Synergus* species

For the identification of EP *Synergus* species the following key is proposed (Schwéger *et al.* 2015a).

Key to Eastern Palearctic *Synergus* species

1. Radial cell of fore wing entirely closed (Fig. 130) ……………………......……………….……….... 3

– Radial cell of fore wing partially or entirely open (Fig. 131) ………………........……….……... 2

2. Radial cell of fore wing entirely open, R1 and Rs do not reach wing margin ……………………….………………………………………………………......………. ***S. castaneus***

– Radial cell partially opened, R1partially running along wing margin …......…… ***S. kawakamii***

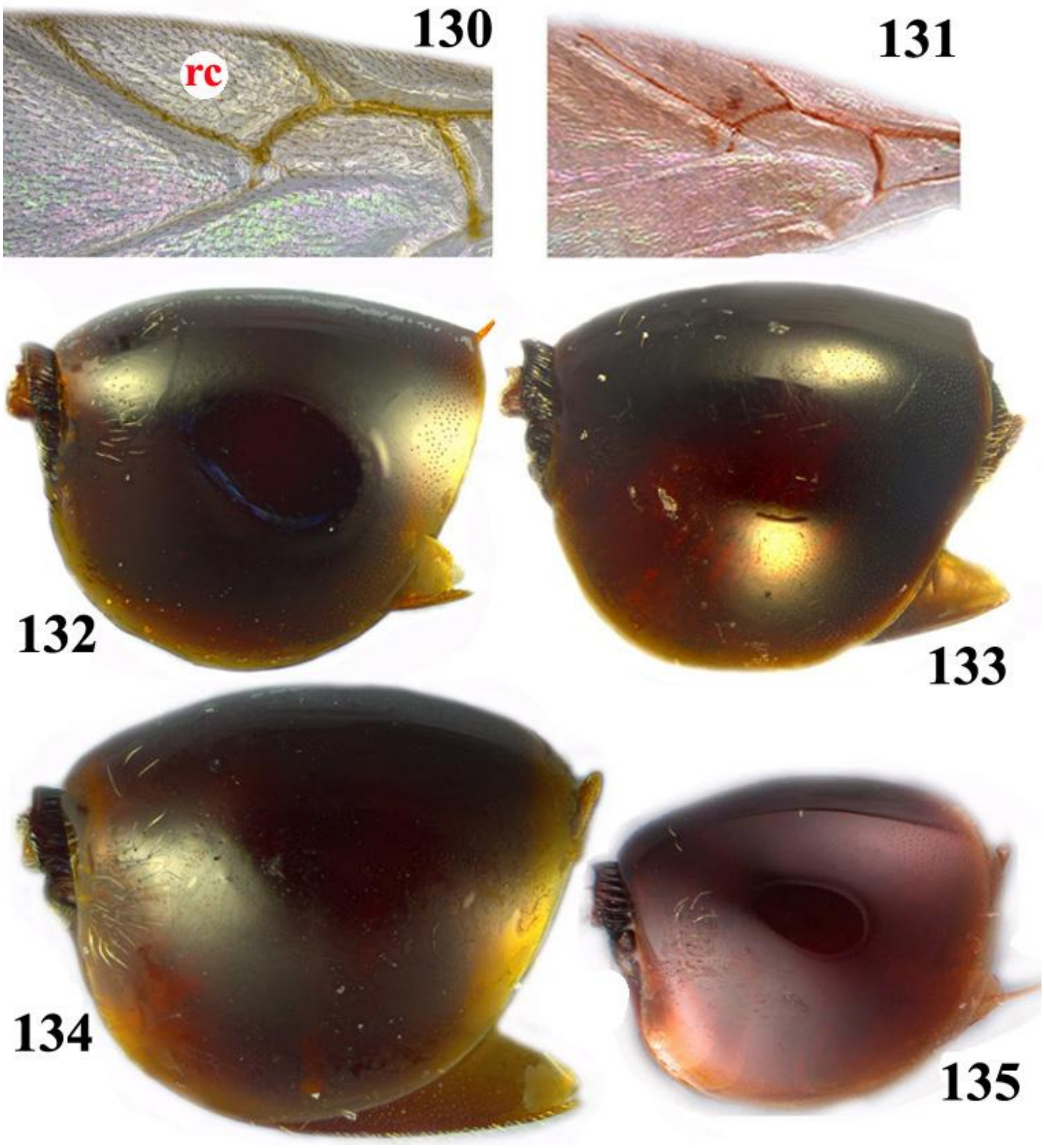
3. Micropunctures on posterior end of syntergite extending laterally to ventral edge, forming a band around syntergite (Figs 132–133) …………….……………………........…………...……… 4

– Micropunctures restricted to a small posterodorsal patch, never extending laterally (Figs 134–135) ………………………………………………………………..…......................……… 10

4. Lateral frontal carinae very indistinct, visible only near toruli; F1 in female weakly curved medially and slightly expanded apically; F1 in male strongly expanded apically and basally, 3.0 times as long as pedicel .... ***S. deqingensis***

– Lateral frontal carinae always present, distinct (Figs 136–138); F1 in female not expanded apically, straight, cylindrical; F1 in male expanded only apically, if basally also than always less expanded than apically ………………………………….........……………..……................. 5

5. Syntergite without antero-lateral patch of setae; lower face in female yellow, F2 in female slightly incised medially …………………………………………………...................... ***S. jezoensis***



FIGURES 130–135. 130–131, female, fore wing, part (rc, radial cell): 130, *Synergus abei*, 131, *S. kawakamii*. 132–135, metasoma, female, lateral view: 132, *S. abei*, 133, S. *changtitangi*, 134, S. *belizinellus*, 135, *S. formosanus*.

– Syntergite with antero-lateral patch of setae, lower face in female black, dark brown or reddish brown, never yellow, F2 in female not incised medially, straight (Figs 139–140, 143) ……….. 6

6. F1 in female 3.0–3.3 times as long as pedicel, 1.25x longer than F2 (Figs 139, 142–143); F1 in male expanded only apically, if expanded basally than only very slightly (Figs 141, 144–145) ………………………………...................……………………………………………… 7

– F1 in female about 2.0 times as long as pedicel, subequal with F2; F1 in male expanded apically and basally 9

7. Posterior band of micropunctures on syntergite broad, dorsally extending to 1/3 of its length; F1 of male expanded only apically (Figs 141, 144) …………………...................….....……… 8

– Posterior band of micropunctures on syntergite narrow, dorsally extending to 1/5–1/7 of its length; F1 of male expanded apically and very slightly basally ……....…………………… ***S. abei***

8. Female head transverse in dorsal view, quadrangular in frontal view (Fig. 137); frontal carina uniformly strong, always reaches lateral ocellus (Fig. 137); F1 in male strongly expanded apically (Fig. 145) …………………………..……......................……………..….. ***S. khazani***

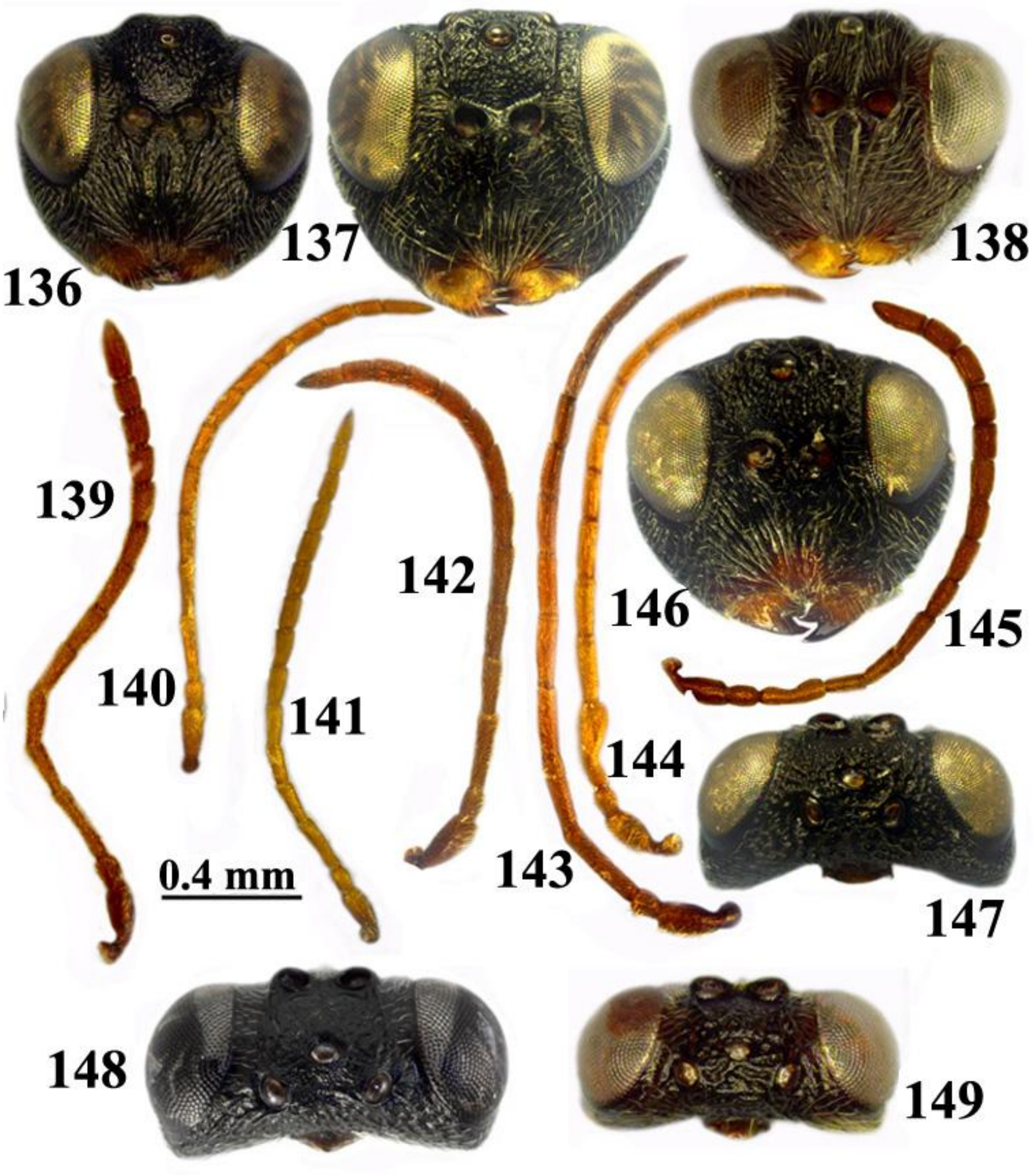
– Female head more robust in dorsal view (Fig. 147), rounded in frontal view (Fig. 146); frontal carina weak, sometimes hardly or not traceable at lateral ocellus or extending to 1/2–2/3 of distance to lateral ocellus (Figs 146–147); F1 in male very weakly expanded apically (Fig. 142) ………………………………………………….......................……………… ***S. changtitangi***

9. Head ovate in frontal view; lower face with strong median carina raised above striae; pedicel in female longer than broad; median mesoscutal impression short, reaching to mid length of mesoscutum and sometimes abruptly broadened posteriorly; scutelar foveae rugose; female syntergite only slightly incised dorsoapically ……………..............…................... ***S. gifuensis***

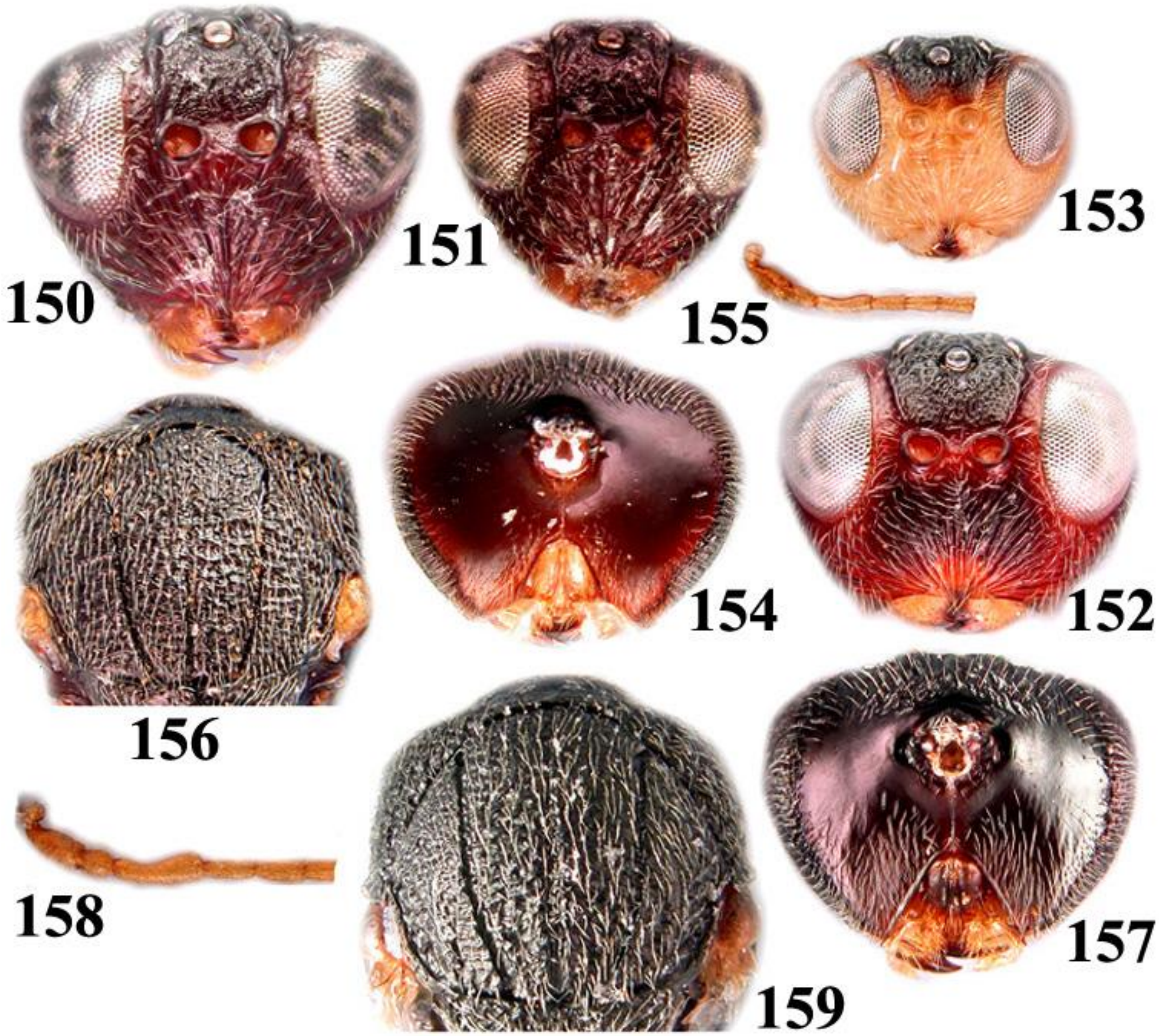
– Head triangular in frontal view; lower face with weak median carina not raised above striae; female pedicel as long as broad; median mesoscutal impression almost complete; scutellar foveae alutaceous; female syntergite strongly incised dorso-apically …......……….. ***S. japonicus***

10. Head in frontal view in females and males, lower space, frons genae partially or entirely, always black or very dark brown; mesosoma black or dark brown …………………......……. 11

– Head in frontal view in females and males, lower space, frons and genae partially or entirely, always light brown or yellowish; mesosoma predominantly reddish brown, never black ......… 13



FIGURES 136–149. 136–138, head, female, frontal view: 136, *S. abei*, 137, *S. khazani*, 138, *S. belizinellus*. 139–145, antenna: 139, *S. abei*, female; 140, *S. belizinellus*, 141, *S. changtitangi*, female, 142, *S. changtitangi*, male, 143, *S. khazani*, female, 144, *S. khazani*, male, 145, *S. abei*, male. 146–147, *S. changtitangi*, head, female: 146, frontal view, 147, dorsal view. 148–149, head, female, dorsal view: 148, *S. ishikarii*, 149, *S. belizinellus*.



FIGURES 150–159. 150–151, *S. naiquanlini*, head, frontal view: 150, female, 151, male. 152–156, *S. formosanus*: 152, head, female, frontal view, 153, head, male, frontal view, 154, head, female, posterior view, 155, male, antenna, part, 156, mesoscutum, dorsal view. 157–159, *S. symbioticus*: 157, head, female, posterior view, 158, antenna, male, part, 159, mesoscutum, dorsal view.

11. Head very delicately coriaceous without striae and deep punctures on frons, vertex and interocellar area; mesoscutum uniformly alutaceous or very delicately coriaceous, without distinct transverse interrupted striae between notauli ……….....…….…………… ***S. hakonensis***

– Head always with rugose sculpture, with distinct deep punctures on frons, vertex and interocellar area, with striae on frons; mesoscutum with strong surface sculpture, coriaceous or rugose, with distinct elevated transverse rugae, especially in between notauli ……..............… 12

12. Female and male head in frontal view trapezoid, height of eye 1.8–1.9x longer than length of malar space; in female POL:OOL:LOL=2.1:1:1.2 (Fig. 148); length of lateral ocellus in male nearly equal to POL; F1 in female 1.3–1.4x longer than F2 …………………….…... ***S. ishikarii***

– Female and male head in frontal view rounded or ovate, height of eye only 1.45x longer than length of malar space; in female POL:OOL:LOL=2.8:1:1.2 (Fig. 149); length of lateral ocellus in male 1.5x shorter than length of POL; F1 in female nearly equal in length to F2 ………………………………………………….………………….……… ***S. belizinellus***

13. Head of female and male in frontal view triangular, higher than broad; genae very narrow, straight aside head in frontal view, never rounded (Figs 150–151) …................... ***S. xialongmeni***

– Head of female and males in frontal view always rounded, always broader than high; gena bucate, in some species partially visible behind eye in frontal view (Figs 152–153) ……..….. 14

14. Head and mesosoma reddish brown ……………………….………………..….. ***S. chinensis***

– Head reddish brown, mesosoma always black or very darkish black ……..……………….. 15

15. Postgena without setae (Fig. 154); F1 in male curved but not expanded apically (Fig. 155); median mesoscutal line deeply impressed in posterior half, extending to 2/3 of mesoscutum, never complete (Fig. 156); mesoscutellum slightly longer than broad …………..... S. ***formosanus***

– Postgena with dense white setae especially along hypostomata (Fig. 157); F1 in male curved and expanded apically (Fig. 158); median mesoscutal line strongly impressed, complete, reaches pronotum (Fig. 159); mesoscutellum 1.4× longer than broad ....…… ***S. symbioticus***

3.3.3. Annotated list of Eastern Palearctic *Synergus* species

All Eastern Palearctic species are given below in alphabetical order, with brief data on their biology, hosts and distribution (Schwéger *et al.* 2015a).

Synergus abei Melika & Schwéger, 2015

This species was reared from undescribed acorn galls on *Q. crispula* and *Q. serrata* (Figs A123, A126) and unknown bud galls (Figs A124–A125) collected from *Q. crispula*. Adults emerged under laboratory conditions during October. Currently known only from Japan (Hokkaido and Kyushu). Diagnosis and detail species description are given in Schwéger *et al.* (2015a).

Synergus belizinellus Schwéger & Melika, 2015

This species was reared mainly from asexual leaf galls of *Belizinella vicina* Kovalev (Fig. A119) collected from *Q. mongolica* and also from two morphotypes of undescribed leaf galls (Figs A121–A122) collected from *Q. dentata* and *Q. crispula*. Adults emerged under laboratory conditions in October-November. Currently known only from the Far East Russia, Primorskij Kraj and Japan (Hokkaido). Diagnosis and detail species description are given in Schwéger *et al.* (2015a).

Synergus brevis (Weld, 1926)

Originally described as *Saphonecrus brevis* Weld, 1926 based on the open radial cell of the forewing (Weld 1926). Currently known from the USA (New Mexico and Arizona) and was reared from *Andricus ruginosus* Bassett galls developing on section *Quercus* of genus *Quercus* oaks (Weld 1926, Burks *et al*. 1979). The holotype female, deposited at the USNM, labeled as “Magdalena, N.M.”, “*Quercus grisea*”, red “Type 27224 USNM”, “*Saphonecrus brevis* Weld”, was examined and the species is transferred to *Synergus* (Schwéger *et al.* 2015b). The radial cell of the forewing is partially open, R1 reaching the wing margin and runs along the margin onto 1/3 of the radial cell length. The frontal carina is strong, complete, and reaches the lateral ocellus; the head is broadened behind the eye in frontal view; the female antenna has 12 flagellomeres. The side of the mesosoma, in dorsal view, is rounded, the lateral pronotal carina is absent; the mesoscutum has strong transverse rugae, the space between the rugae is smooth; the notaulus is complete, reaching the anterior margin of the mesoscutum; the metapleural sulcus is nearly straight, and does not reach the posterior margin of the mesopectus; the tarsal claws are simple; the first metasomal tergite has delicate, indistinct sulci laterally, absent dorsally; the syntergite has a row of white setae anterolaterally, is not incised dorsoposteriorly, and has a narrow band of micropunctures which nearly reaches the ventral edge of the tergite. The combination of characters is more typical for *Synergus*, thus, we transferred this species to *Synergus* as *Synergus brevis* (Weld, 1926) (Schwéger *et al.* 2015a).

Synergus changtitangi Melika & Schwéger, 2015

This species was reared from undescribed multilocular stem swelling-like galls (Fig. A127) collected from *Q. serrata.* Adults emerged during March. Currently known from Taiwan (Nantou County). Diagnosis and detail species description are given in Schwéger *et al.* (2015a).

Synergus chinensis Melika, Ács & Bechtold, 2014

This species was described from north-eastern China (Beijing Province), reared from unknown cynipid acorn, leaf and bud galls (Melika *et al*. 2004). Later it was found in South Korea (Abe *et al.* 2007). Kovalev (1965) mentioned *S. gallaepomiformis* (Boyer de Fonscolombe) for the Far East of Russia, which was reared from asexual galls of *Andricus hakonensis* (= *A. symbioticus,* = *A. attractus*). We strongly doubt this identification. On the basis of the adult description given by Kovalev, these specimens belong to *S. chinensis* (Melika *et al*. 2004) which falls into a subclade with *S. symbioticus* and can be easily distinguished from the latter by some bright diagnostic characters given in the key to *Synergus*. Currently known from China, South Korea and Russia.

Synergus formosanus Schwéger & Melika, 2015

This species was reared only from the asexual galls of *Trichagalma formosana* (Fig. A118) on *Q. variabilis*, adults emerge under laboratory conditions in October. Currently known from Taiwan (Nantou County). Diagnosis and detail species description are given in Schwéger *et al.* (2015a).

Synergus gifuensis Ashmead, 1904

Synergus gifuensis was described from three specimens (Ashmead 1904). The type female labelled as ”Y, Nawa, Gifu, Jap. det. 1902”, red label ”Female Type No.7304 USNM”, Ashmead’s handwritten label ”*Synergus gifuensis*” was examined by us. Abe (1990) referred to this species as *Synergus japonicus* type B. which appeared to be univoltine and arrhenotokous. Adults emerge from asexual galls of *Andricus mukaigawae* in early June. Galls of *A. mukaigawae* inhabited by *S. gifuensis* are usually larger than those inhabited by *S. japonicus*, and the inquiline larval cells are usually separated by a woody wall inside the host gall (Abe 1990, 1992a, Pujade-Villar *et al.* 2002). A detailed description of the adults, species diagnosis and additional data on hosts (asexual galls of *A. kashiwaphilus*), was given by Pujade-Villar *et al.* (2014b). Wasps were reared from galls of *A. mukaigawae*, collected in Japan (Hokkaido) and the Far East Russia (Primorskij Kraj, Khazan Lake).

Synergus hakonensis Ashmead, 1904

Synergus hakonensis is a valid species, most closely resembles *S. ishikarii* and *S. belizinellus* by the rounded head in frontal view. In *S. hakonensis* the head is very delicately coriaceous, without striae and deep punctures on the frons, vertex and interocellar area; the mesoscutum is uniformly alutaceous or very delicately coriaceous, without distinct transverse interrupted striae between notauli, while in *S. ishikarii* and *S. belizinellus* the head is always with rugose sculpture, with distinct deep punctures on the frons, vertex and interocellar area, with striae on the frons; the mesoscutum with strong surface sculpture, coriaceous or rugose, with distinct elevated transverse rugae, especially in between notauli (for more diagnostic characters see also the key to species). Currently the species is known only from the one type specimen collected in Japan (Schwéger *et al.* 2015a).

Synergus hupingshanensis (Liu, Yang & Zhu, 2012)

In this species, the female antenna has 12 flagellomeres, the tarsal claws have a triangular basal lobe; and the frontal carina is weak, complete, and reaches the torulus. The radial cell of the fore wing is partially open, with R1 reaching the wing margin and running a short distance along the margin. It is known from China (Guanshan). The examination of the detailed description and illustrations of this species showed that it is not a *Saphonecrus* but a *Synergus* species: *Synergus hupingshanensis* (Liu, Yang & Zhu) which belongs to the group of *Synergus* species (*Synergus castaneus*, *S. plagiotrochi* and *S. kawakamii*) with partially open radial cell of the fore wing (Schwéger *et al*. 2015a). This species is associated with galls developing on *Castanopsis carlesii* which from Liu *et al*. (2012) never reared any gallwasp, thus they do not exclude the possibility that *S. hupingshanensis* might be a gall inducer (Liu *et al*. 2012). Such is the case with *Synergus itoensis* Abe, Ide & Wachi (Abe *et al*. 2011).

Synergus ishikarii Melika & Schwéger, 2015

This species was reared from asexual leaf galls of *Ussuraspis* sp. (Fig. A120) and undescribed leaf galls (Fig. A121) on *Q. dentata* and unknown leaf galls (Fig. A122) collected from *Q. crispula*. Adults emerged under laboratory conditions in October-November. Currently known from Japan (Hokkaido). Diagnosis and detailed species description are given in Schwéger *et al.* (2015a).

Synergus iwatensis Shinji, 1941

Japan. The type lost, status is uncertain (Abe *et al*. 2007).

Synergus japonicus Walker, 1874

Detailed re-description, diagnosis, and data on biology and distribution were provided by Pujade-Villar *et al*. (2014b). The biology of the species was described in details in Abe (1990, 1992a). For a long time the species was known only from Japan, but recently also recorded from China (Pujade-Villar *et al*. 2014b). We collected and reared *S. japonicus* in large numbers from galls of *A. kashiwaphilus* in the Far East Russia (Primorskij Kraj, Khazan Lake). Currently the species is known from Japan, China and Russia (Schwéger *et al.* 2015a).

Synergus jezoensis Uchida & Sakagami, 1948

This species was recently re-validated, types were examined and a detail re-description with diagnosis was provided by Pujade-Villar *et al*. (2014b). Species is known from Japan and China (Zhejiang); biology is unknown (Pujade-Villar *et al*. 2014b).

Synergus kawakamii Tang & Melika, 2015

This species was reared from undescribed irregular spheric galls on *Castanopsis kawakamii*. Currently known from Taiwan (Hualien County). It is the first *Synergus* species reared from galls on *Castanopsis*. Diagnosis and detail species description are given in Schwéger *et al.* (2015a).

Synergus khazani Melika & Schwéger, 2015

Most specimens were reared from the asexual galls of *A. kashiwaphilus* (Fig. A115) and *A. mukaigawae* (Fig. A116), collected from *Q. mongolica* and *Q. dentata*; few specimens were obtained from an unknown bud gall (Fig. A124) and unknown acorn gall (Fig. A126), both collected from *Q. crispula*. Adults emerge under laboratory conditions in October-November. Currently known from the Far East Russia (Primorskij Kraj, Khazan Lake and Vityaz Bay), Japan (Hokkaido) (Schwéger *et al.* 2015a) and China (Pujade-Villar *et al.* 2016). Diagnosis and detail species description are given in Schwéger *et al.* (2015a).

Synergus mizunarae Shinji, 1940

Japan. The type is lost; status is uncertain (Abe *et al*. 2007).

Synergus symbioticus Schwéger & Melika, 2015

This species was reared from the asexual galls of *Andricus hakonensis* (= *A. symbioticus*) (Fig. A117) and *A. kashiwaphilus* on *Q. dentata* and *Q. mongolica* subsp. *crispula*. Adults emerge in October. Currently known from Japan (Hokkaido) and the Far East Russia (vicinity of Vladivostok). Diagnosis and detail species description are given in Schwéger *et al.* (2015a).

Synergus xialongmeni Melika, Ács & Bechtold, 2004

Currently known from China (Beijing Province), reared from unknown cynipid acorn, leaf and bud galls (Melika *et al.* 2004). This species shows some morphological similarity to *S. belizinellus* and *S. ishikarii*.

Synergus yukawai (Wachi, Ide & Abe, 2011)

This species known from Japan (Honshu and Kyushu) was reared from a gall midge *Ametrodiplosis acutissima* (Monzen) (Diptera: Cecidomyiidae) galls on *Q. acutissima* (*Quercus* section Cerris) (Wachi *et al*. 2011b). The species has a strong, complete lateral frontal carina, and thus, it is not a *Saphonecrus* and was transferred by us to *Synergus*. The species belongs to the group of *Synergus* species with partially open radial cell of the fore wing, such as *Synergus castaneus*, *S. plagiotrochi* and *S. kawakamii* (Schwéger *et al*. 2015a).

3.4. Phylogenetics of Synergini sensu stricto

Sixty taxa were included in the phylogenetic reconstruction (Table 8) of Palearctic species of Synergini sensu stricto (Pénzes *et al.* 2012). The phylogenetic analysis is based on 1,240 aligned sequence positions. The phylogenetic position of *Synophrus, Lithosaphonecrus, Saphonecrus* and *Ufo* has been recently re-appraised and established (Bozsó *et al*. 2014; Melika *et al*. 2005, 2007, 2012; Pénzes *et al*. 2009, 2012; Nieves-Aldrey & Butterill 2014). Bozsó *et al*. (2014) included sequences from the newly described *Saphonecrus* species, too. Similarly to the previous studies, *Lithosaphonecrus, Ufo, Synergus* and *Synophrus* were recovered as monophyletic groups (genera) in contrast to *Saphonecrus* (Fig. 160).

Four basal clades were established (Pénzes *et al.* 2012, Bozsó *et al.* 2014), *Synophrus, Saphonecrus* #1, *Saphonecrus*-#2 and a large clade with all the remaining lineages, although their relationships are generally unresolved. The latter large clade is divided into several lineages, including *Ufo*, *Lithosaphonecrus*, five *Saphonecrus* lineages from EP and WP, and *Synergus*.

Table 8. GenBank accession number of haplotype sequences used in the phylogenetic reconstructions. Names between quotation marks refer to the labels used in the previous referred studies. Note that samples S27 and S57 appeared as *Saphonecrus shirokashicola* in the earlier literature and corrected in Schwéger *et al.* (2015a, b).

Lineage	***cox1* haplotype**	**28S D2 haplotype**	**References**
Lithosaphonecrus dakengi	KC899797	KC899801	Bozsó *et al.* 2015
Lithosaphonecrus formosanus	KC899798	KC899802	Bozsó *et al.* 2015
Lithosaphonecrus huisuni	KC899795	KC899799	Bozsó *et al.* 2015
Lithosaphonecrus yunnani	KC899796	KC899800	Bozsó *et al.* 2015
Rhoophilus loewi (outgroup)	EF486876	EF487123	Ács *et al.* 2010
Saphonecrus barbotini	EF486877	EF487124	Ács *et al.* 2010
Saphonecrus chinensis “S30”	KF532109	KF532097	Bozsó *et al.* 2014
Saphonecrus connatus	EF486878	EF487125	Ács *et al.* 2010
Saphonecrus gallaepomiformis	EF486881	EF487131	Ács *et al.* 2010
Saphonecrus gilvus “TWTl12”	JX468364	JX468369	Melika *et al.* 2012
Saphonecrus globosus “S18”	KF532107	KF532094	Bozsó *et al.* 2014
Saphonecrus haimi	EF486879	EF487126	Ács *et al.* 2010
Saphonecrus lithocarpii “S32”	KF532110	KF532098	Bozsó *et al.* 2014
Saphonecrus longinuxi”S 2,JP02”	JX468362	JX468368	Melika *et al.* 2012
Saphonecrus longinuxi “S9, JP02”	JX468363	JX468368	Melika *et al.* 2012
Saphonecrus morii “S11”	KF532105	KF532092	Bozsó *et al.* 2014
Saphonecrus morii “S49”	KF532116	KF532092	Bozsó *et al.* 2014
Saphonecrus nantoui “S23”	KF532108	KF532095	Bozsó *et al.* 2014
Saphonecrus nantoui “S35”	KF532112	KF532095	Bozsó *et al.* 2014
Saphonecrus nichollsi “S36”	KF532113	KF532100	Bozsó *et al.* 2014
Saphonecrus pachylomai ”S48”	KF532115	KF532102	Bozsó *et al.* 2014
Saphonecrus saliciniai” S57”	KF532122	JX468371	Bozsó *et al.* 2014
Saphonecrus saliciniai “S27”	KF532121	KF532091	Bozsó *et al.* 2014
Saphonecrus shanzhukui “S15”	KF532106	KF532093	Bozsó *et al.* 2014
Saphonecrus shanzhukui “S46”	KF532114	KF532101	Bozsó *et al.* 2014
Saphonecrus shirakashii	JX468365	JX468370	Melika *et al.* 2012
Saphonecrus shirokashicola	JX468366	JX468371	Bozsó *et al.* 2014; Melika *et al.* 2012
Saphonecrus symbioticus “S50”	KF532117	KF532103	Bozsó *et al.* 2014
Saphonecrus symbioticus “S51”	KF532118	KF532103	Bozsó *et al.* 2014
Saphonecrus taitungi “S34”	KF532111	KF532099	Bozsó *et al.* 2014
Saphonecrus undulatus	EF486883	EF487133	Ács *et al.* 2010
Synergus abei	KR270551	KR270534	Schwéger *et al.* 2015a
Synergus acsi	EF486884	EF487134	Ács *et al.* 2010
Synergus belizinellus	KR270555	KR270536	Schwéger *et al.* 2015a
Synergus castaneus	KC533850	KC533844	Bernardo *et al.* 2013

Lineage	***cox1* haplotype**	**28S D2 haplotype**	**References**
Synergus chinensis	EF486890	EF487140	Ács *et al.* 2010
Synergus consobrinus	EF486955	EF487190	Ács *et al.* 2010
Synergus crassicornis	EF486898	EF487147	Ács *et al.* 2010
Synergus incrassatus	EF486925	EF487165	Ács *et al.* 2010
Synergus japonicus	KR270560	EF487167	Schwéger *et al.* 2015a
Synergus formosanus	KR270545	KR270532	Schwéger *et al.* 2015a
Synergus ishikarii	KR270548	KR270533	Schwéger *et al.* 2015a
Synergus khazani	KR270557	KR270537	Schwéger *et al.* 2015a
Synergus mikoi	EF486928	EF487169	Ács *et al.* 2010
Synergus plagiotrochi	EF486952	EF487188	Ács *et al.* 2010
Synergus symbioticus “S7”	KR270540	KR270530	Schwéger *et al.* 2015a
Synergus symbioticus “S122”	KR270541	KR270530	Schwéger *et al.* 2015a
Synergus thaumacerus	EF486957	EF487222	Ács *et al.* 2010
Synergus xiaolongmeni	EF486968	EF487220	Ács *et al.* 2010
Synergus sp “MOTU2 S110”	HM574230	HM574142	Kaartinen *et al.* 2010
Synergus sp “MOTU4 S30”	HM574169	HM574132	Kaartinen *et al.* 2010
Synergus sp. “SP10 flavipes”	EF486903	EF487151	Ács *et al.* 2010
Synophrus olivieri	EF579725	EF583959	Ács *et al.* 2010; Pénzes et al. 2009
Synophrus pilulae	EF579716	EF487224	Ács *et al.* 2010; Pénzes *et al.* 2009
Synophrus politus	EF579710	EF487223	Ács *et al.* 2010; Pénzes *et al.* 2009
Ufo cerroneuroteri” S8”	JX468357	JX468367	Melika *et al.* 2012
Ufo cerroneuroteri” S14”	JX468358	JX468367	Melika *et al.* 2012
Ufo nipponicus “S38”	JX468359	JX468367	Melika *et al.* 2012
Ufo nipponicus “S39”	JX468360	JX468367	Melika *et al.* 2012
Ufo nipponicus “S40”	JX468361	JX468367	Melika *et al.* 2012

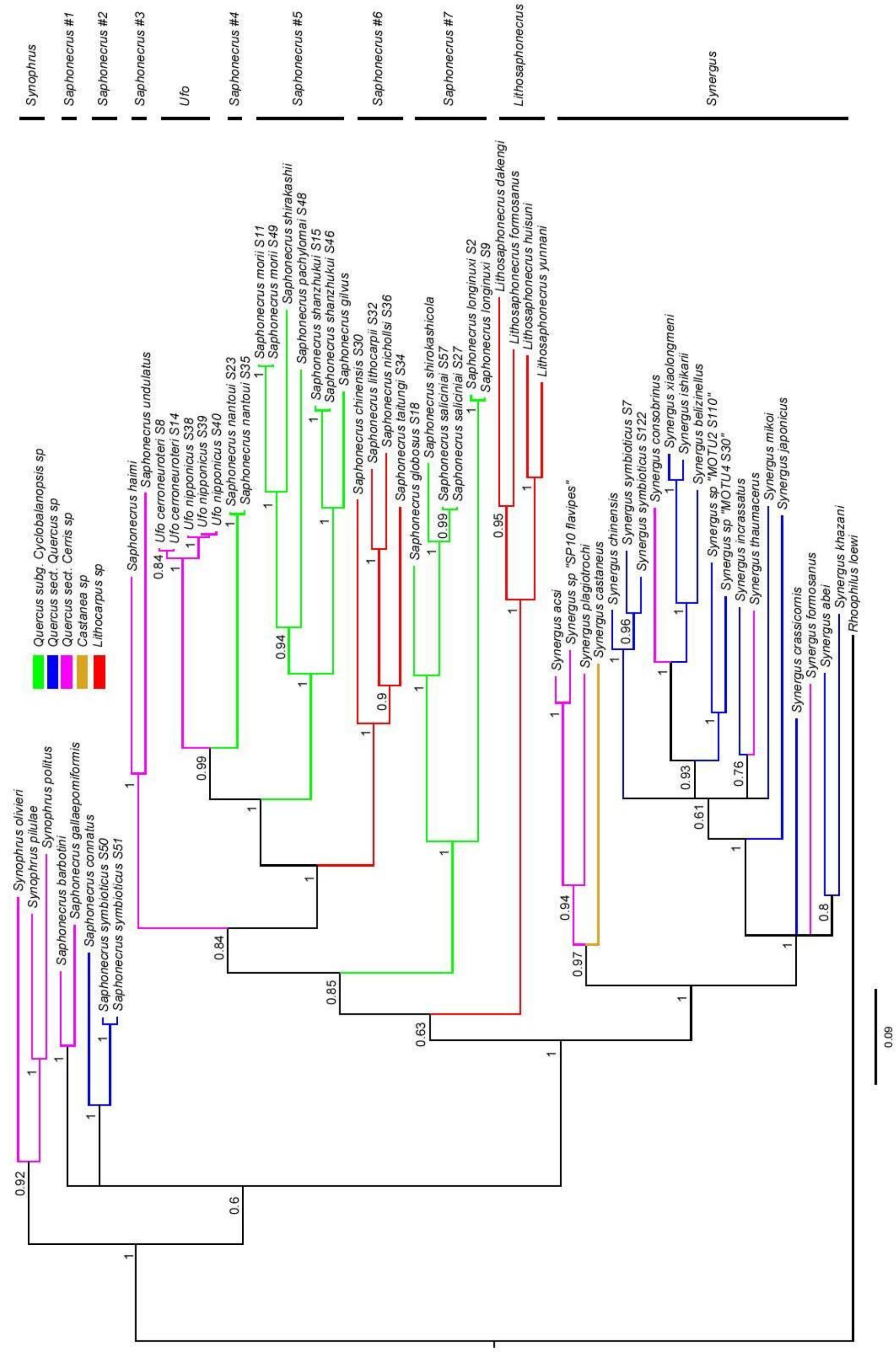


FIGURE 160. Bayesian majority rule consensus phylogeny of *Saphonecrus* and *Synergus*. Host plant associations are coded by colors. Numbers at nodes indicate estimated posteriori clade probabilities (Schwéger *et al.* 2015a, b).

The division of the genus *Synergus* into section I and section II (Mayr 1872) appeared to be artificial, with each section being polyphyletic (Ács *et al.* 2010). Our phylogenetic tree support this conclusion and the newly described species of *Synergus* from the EP span the *Synergus* phylogenetic tree: species allocated morphologically to Section I (*S. abei*, *S. changtitangi*, *S. khazani*) are intermixed with those allocated to Section II (*S. belizinellus, S. formosanus, S. ishikarii S. symbioticus*) (Fig. 160).

Concerning the monophyly of *Synergus*, it is important to state that only WP and EP *Synergus* species were included in the analyses, so the worldwide monophyly of *Synergus* remains to be tested. Although the reconstruction included a subset of *Synergus* examined in detail, Palearctic *Synergus* remains monophyletic (Schwéger *et al*. 2015a). The eight newly described EP *Synergus* species fall into 6 distinct clades, although sistergroup relationships remain uncertain in many cases (Fig. 160). *Synergus belizinellus*, *S. ishikarii*, and *S. xialongmeni* fall into one subclade. These species also form a distinct morpho-group, and characterized by a rugose head, the frons and vertex are with deep punctures and striae, the mesoscutum with strong surface sculpture. Another distinct subclade, *Synergus chinensis* and *S. symbioticus*, also possess distinct set of morphological character states: the head of the female and male in frontal view always is rounded and broader than high; the gena is bucate and partially visible behind eye in frontal view. On the other hand, *S. japonicus* and *S. khazani*, which are falling into different subclades, are showing similarity in some morpho-characters: the dull rugose mesoscutum, deep scutellar foveae, rugose frons and vertex, strong carinae on the lower face. Grouping of EP *Synergus* species into different subclades (Fig. 160) not necessarily followed by a distinct set of morpho-characters. Host associations are interpreted in Discussion.

3.5. Eastern Palearctic Cynipini

3.5.1. Eastern Palearctic oak gallwasps

Herein listed 85 EP species of Cynipini trophically associated with ten *Quercus* subgenus *Quercus* species, 9 *Quercus* subgenus *Cyclobalanopsis*, 2 *Castanopsis*, 6 *Castanea* and 1 *Lithocarpus* species (unpublished results). The oak gallwasp faunas of WP, EP and Nearctic are very peculiar and each biogeographical region possesses with its own distinct species diversity without any overlap. The number of known Cynipini species in the WP is 2 times higher than the number of species described from the EP. However, the EP fauna is much less studied and further research definitely will reveal a great number of new species. It is expected that the host diversity will also increases with further research. Currently many more gall morphotypes are known which are differ from the described species and might well represent new, undescribed species. The annotated list of EP Cynipini with including species known from the Oriental Region is given in Appendix 9.2., while the list of species with uncertain status is given in Appendix 9.3 (unpublished results).

The number of recognised species in each genus of Cynipini in WP and EP are given in Table 9.

Table 9. Comparison of Western and Eastern Palearctic Cynipini oak gallwasp fauna

Genus	**WP**	**EP**
Andricus Hartig, 1840	99	16
Aphelonyx Mayr, 1881	3	–
Belizinella Kovalev, 1965	–	2
Biorhiza Westwood, 1840	1	1
Callirhytis Foerster, 1869	6	1
Cerroneuroterus Melika & Pujade-Villar, 2009	6	3
Chilaspis Mayr, 1881	2	–
Cyclocynips Melika, Tang, &Sinclair, 2013	–	2
Cycloneuroterus Melika & Tang, 2011	–	17
Cynips Linnaeus, 1758	9	1
Dryocosmus Giraud, 1859	6	12
Latuspina Monzen, 1954	–	9
Neuroterus Hartig, 1840	6	7
Plagiotrochus Mayr, 1881	14	7
Pseudoneuroterus Kinsey, 1923	4	–
Trichagalma Mayr, 1907	–	3
Trigonaspis Hartig, 1840	5	3
Ussuraspis Kovalev, 1965	–	1
TOTAL	**161**	**85**

4. DISCUSSION

4.1 Integrative taxonomy and phylogeny of *Saphonecrus* and *Synergus* species

Based on combined analyses of morphological, molecular and biological data, Ronquist *et al.* (2015) rejected the monophyly of inquiline gallwasps (Synergini). Tribe Diastrophini was established for two inquiline genus (*Synophromorpha* and *Periclistus*) and Rosaceae gallers with strong phylogenetic support. The Fagaceae host plant and overwhelmingly Cynipini gall associated inquilines (Synergini sensu lato) were divided into two distinct lineages as follows: Synergini sensu stricto including *Lithosaphonecrus*, *Saphonecrus*, *Synergus*, *Synophrus* and *Ufo* genera (Synergini sensu stricto) and Ceroptresini (one genus, Ceroptres) with strong support (Ronquist *et al.* 2015).

Within the tribe Synergini there is some contradiction between the morphology-based taxonomy and the molecular phylogeny when considering the classification above the species level, especially striking in the largest genera, *Synergus* and *Saphonecrus* (Melika 2006, Pénzes *et al.* 2009, Ács *et al.* 2010).

All of the recently described new EP *Saphonecrus* and *Synergus* species are supported by distinct mitochondrial DNA haplotypes, which support the description of novel species established by the morphology. On the other hand, there is some contradiction between morphology-based taxonomy and molecular phylogeny considering the classification above the species level (Schwéger *et al*. 2015a, b).

Although the presented phylogenetic tree (Fig. 106) is ambiguous in many details, it suggests clearly distinct groups of species with high support. However, in some cases, different clades include species with the same group of diagnostic characters, while other clades include species with different characteristics which can be found in species which belong to different clades. For instance in case of *Saphonecrus shirakashii* and *Saphonecrus shirokashicola*, which have a slightly different morphological character states, belong to two different distantly related lineages within Synergini (Figs 118-119, 125-126, 160). Some previously described EP species appear to be erroneously included in *Saphonecrus* and were moved to *Synergus*. Besides these inconsequences, all of the described new EP *Saphonecrus* species (Schwéger *et al.* 2015b) are characterized by distinct mitochondrial *coxI* DNA haplotypes (barcodes), which is concordant to the discrimination of novel species established by the morphology. More reliable estimation of evolutionary relationships and corresponding taxonomy requires further research. Owing to these limitations, we decided to leave all the newly described species within *Saphonecrus* because it is too early to establish new genera until the basic divisions within *Saphonecrus* are solved (Schwéger *et al.* 2015b).

The genus *Lithosaphonecrus* Tang, Melika & Bozsó, with four species, which most closely related to *Saphonecrus* and forms a distinct lineage within Synergini, was described from China and Taiwan (Bozsó *et al*. 2015, online version in 2013). *Lithonecrus* Nieves-Aldrey & Butterill, with one species *L. papuanus* Nieves-Aldrey & Butterill, collected from *Lithocarpus celebicus*, was described from Papua New Guinea (Nieves-Aldrey & Butterill 2014), was synonymized to *Lithosaphonecrus* (Schwéger *et al.* 2015a), as *Lithosaphonecrus papuanus* (Nieves-Aldrey & Butterill, 2014). The known geographic distribution of *Lithosaphonecrus* is expanded in this way.

4.2. Phylogenetics of Synergini sensu stricto

The phylogenetic position of *Lithosaphonecrus*, *Saphonecrus*, *Synophrus* and *Ufo* has recently been re-appraised and re-established with a more detailed taxon sampling (Bozsó *et al*. 2014, 2015, Melika *et al*. 2005, 2007, 2012; Pénzes *et al*. 2012).

The current phylogenetic and morphological examination of the EP *Synergus* supports Ács *et al*. (2010)'s conclusion that palearctic *Synergus* comprise a monophyletic group, with previously known and here described EP species nested among the WP species. There is thus no evidence that EP and WP *Synergus* species represent independent regional radiations. However, the monophyly of worldwide *Synergus* must be treated carefully. Many species assigned to *Synergus* in the Nearctic show significant morphological differences from palearctic taxa (Ács *et al*. 2010, Pénzes *et al*. 2012, Melika *et al*. 2012, Bozsó *et al*. 2014, 2015). Preliminary unpublished analysis shows at least three distinct groups within Nearctic *Synergus,* and assessment of their status, and of the genus as a whole, requires a new phylogenetic re-analysis (unpublished results).

The monophyletic *Synergus* is nested within *Saphonecrus* as well as the *Ufo* and *Lithosaphonecrus* genera (Fig. 160) (Melika *et al*. 2012, Bozsó *et al*. 2014, 2015), according to the two gene sequence based molecular phylogeny. That is, *Saphonecrus* does not seem to be monophyletic. Molecular phylogenetic analyses of Palearctic Synergini (Pénzes *et al.* 2012, Bozsó *et al.* 2014, Bozsó 2015, Schwéger *et al*. 2015a, b; Fig. 160) suggested three basal lineages, although their sister-group relationships are unresolved. Two of these clades include *Saphonecrus* species described recently (Schwéger *et al*. 2015a). "*Saphonecrus* #2", with S. *connatus* and *S. symbioticus*, seem to represent independent divergences from all others that share a common ancestor (Fig. 160). This lineage is associated with the white oaks section of *Quercus*. All the molecular data, together with some morphological peculiarities, suggests that it is clearly a distinct unit, different from the "barbotini-gallaepomiformis" ("*Saphonecrus* #1", Pénzes *et al*. 2009, Ács *et al*. 2010) associated with section Cerris and other *Saphonecrus* clades discussed below.

According to the host plant associations, the third clade (Fig. 160) may represent a large eastern radiation and can be divided into several further lineages. Some of these include *Saphonecrus* species exclusively (*Saphonecrus* #3-#7, Fig. 160, Bozsó *et al.* 2014). *Saphonecrus haimi* and *S. undulatus* (Saphonecrus #3), known from *Quercus* section Cerris hosts, may be the unique western representative of the eastern radiation on different host plant lineages (Bozsó *et al*. 2014). On the basis of molecular evidence and also morphological peculiar characters, the "undulatus-haimi" lineage is very distant from the western "barbotini-gallaepomiformis" (Saphonecrus #1) and "connatus" (Saphonecrus #2) clades (Bozsó *et al*. 2014).

Our phylogeny may suggest a radiation on *Lithocarpus* hosts (*Saphonecrus* #6). Furthermore, the *Cerris* section specific *Ufo* belong to a well-supported clade with members associated with *Quercus* subgenus *Cyclobalanopsis* exclusively (*Saphonecrus* #4-#5). This clade includes *Saphonecrus shirakashii* and five newly described species. There is another clade on *Quercus* subgenus *Cyclobalanopsis* hosts (*Saphonecrus* #7), that includes *Saphonecrus shirokashicola* and three new species. However, owing to the limitations of our reconstruction, it is not clear at present whether these host-specific lineages represent independent radiations (Bozsó *et al*. 2014, 2015).

Of the 27 *Saphonecrus* species for which the host gall and host plant associations are known, represented partly in the phylogenetic analysis, 11 species associate with hosts developing on *Quercus* subgenus *Quercus*, 12 species with hosts developing on *Quercus* subgenus *Cyclobalanopsis*, and 4 species associate with *Lithocarpus* (Table 2). The majority of Eastern Palearctic *Saphonecrus* species associate with galls developing on *Quercus* subgenus *Cyclobalanopsis* and *Lithocarpus* species, form distinct subclades (Bozsó *et al*. 2014, 2015). One species, *Saphonecrus hupingshanensis* Liu, Yang & Zhu, was known to associate with galls developing on *Castanopsis* (Liu *et al*. 2012), however, based on the morphological examination, it was transferred herein to *Synergus*, thus currently no *Saphonecrus* species are known to associate with the *Castanea*-*Castanopsis* lineage of Fagaceae.

Of 14 Eastern Palearctic *Synergus* species for which the host gall and host plant associations are known, 11 species associated with hosts developing on *Quercus* subgenus *Quercus* (Table 2). One species, *S. itoensis* is a gall-inducer on acorns of *Quercus* subgenus *Cyclobalanopsis*. Two *Synergus* species with opened or partially opened radial cell of the fore wing, *S. kawakamii* and *S. castaneus*, could not be placed reliably on the phylogenetic tree. None-Synergus cynipid inquilines are known to associate with oak galls (Cynipini) developing on *Castanopsis* and *Lithocarpus*. *Saphonecrus excisus* (Kieffer), described from Bengal, *Lithosaphonecrus* species from China, Taiwan and Papua New Guinea are known to associate with *Lithocarpus* (Bozsó *et al*. 2013, Nieves-Aldrey & Butterill 2014). In spite of the recent discovery of a rich oak gallwasp fauna associated with non-Quercus Fagaceae, with the exceptions of *S. itoensis* (on *Cyclobalanopsis*) and *S. kawakamii* (*Castanopsis*) no other *Synergus* species are known to be associated with galls developing on *Quercus* subgenus *Cyclobalanopsis*, *Castanopsis* and *Lithocarpus*. On the other hand, very few *Saphonecrus*, *Lithosaphonecrus* and *Saphonecrus*-like species have been reared from galls of *Andricus*, *Cerroneuroterus*, *Latuspina*, *Plagiotrochus*, and *Trichagalma* genera of Cynipini that associate with *Quercus* subgenus *Quercus* species - in galls induced by these Cynipini, only *Synergus* and *Ufo* species have so far been found.

Futher research is needed to decide whether the *Synergus* and *Saphonecrus*-like inquilines have preferences in host gall and associate host plant and if so, whether such preferences reflect fundamental evolutionary trends in host tracking or codiversification, as observed for the Cynipini gallwasps (Cook *et al*. 2002, Stone *et al*. 2009). A deep evolutionary split was supposed to be present in host plant associations of inquilines, particularly those of the Synergus-complex (Ács *et al*. 2010). However, recent studies suggest examples for different independent radiations on the same host lineages (Bozsó *et al*. 2014). The most striking example is provided by the two *Saphonecrus* lineages present on *Lithocarpus*, one of which was described as a new genus, *Lithosaphonecrus* (Bozsó *et al*. 2015, online in 2013]). The early split within the Fagaceae between *Quercus* and *Lithocarpus* (Oh & Manos 2008) is not reflected in the inquiline phylogeny. Furthermore, the section Cerris-specific, eastern *Ufo* and the western “undulatus-haimi” clade seem to be embedded in the eastern clade, characteristic to the hosts from subgenus *Cyclobalanopsis* of *Quercus* and *Lithocarpus*, all known from the EP. Further research is needed to clarify host shifting events in cynipid inquilines.

4.3. Eastern Palearctic oak gall inducers

Oak gallwasps (Hymenoptera: Cynipidae: Cynipini) are by far the most species-rich group of gallwasps (Csóka *et al*. 2005, Ronquist *et al*. 2015; Table 1). Although the EP fauna is less known, it has probably large species richness.

From 85 EP Cynipini species about the half (49 species) associate with *Quercus* subgenus *Quercus*, while 25 species with *Quercus* subgenus *Cyclobalanopsis* and only eight species known to associate with the rest three oak related Fagaceae genera, *Castanea*, *Castanopsis* and *Lithocarpus* (Abe *et al*. 2014a, b, Ide *et al.* 2010, 2012, 2013, 2016, Melika *et al*. 2011, 2013, Tang *et al.* 2011a, b).

Of the ten described EP species of *Dryocosmus* two species (*D. sakureiensis* Ide, Wachi & Abe, *D. sefuriensis* Ide, Wachi & Abe) are associated with *Cyclobalanopsis*, two further species (*D. nanlingensis* Abe, Ide, & Odagiri, *D. okajimai* Abe, Ide, Konishi & Ueno) are probably associated with *Cyclobalanopsis*, four species (*D. carlesiae* Tang & Melika, *D. pentagonalis* Melika & Tang, *D. testisimilis* Tang & Melika, *D. triangularis* Melika & Tang) are associated with *Castanopsis*, and two species (*D. kuriphilus* (Yasumatsu), and *D. zhuili* Liu & Zhu) are associated with *Castanea* (Abe *et al*. 2014a, b, Ide *et al.* 2010, 2012, 2013, Melika *et al.* 2011, 2013, Tang *et al*. 2011a, b, Zhu *et al*. 2015). Other 12 new *Dryocosmus* species are under description which from five species associates with *Castanopsis* and other seven species with *Cyclobalanopsis*. The genus *Dryocosmus* with its current classification and limits undoubtedly forms a polyphyletic group, as is discussed in detail by Melika *et al.* (2011). Palearctic *Dryocosmus* contains at least three major groups – *kuriphilus* and other East Asian species, and two WP groups consisting of *mayri*/*caspiensis* and related taxa, and *cerriphilus*. The morphological and genetic diversity of East Asian *Dryocosmus* would also imply that Asian members of this genus may reperesent multiple distinct lineages. Hence, further phylogenetic analysis involving all known *Dryocosmus* species is necessary to redefine “true” *Dryocosmus*, alongside detailed examination of morphological character states in each lineage (Melika *et al*. 2011).

Most oak gallwasps are cyclically parthenogenetic, with obligate alternation between a sexual generation involving males and females that usually occurs at the same time as the flush of new growth on host plants in spring, and the asexual generation with only parthenogenetic females occurring in winter (Stone *et al.* 2002). A proportion of gallwasp taxa are only known from one of these two generations, although a recent study confirmed that many species known only from an asexual generation do also possess a sexual generation (Stone *et al.* 2008). In all cases where the sexual and asexual generations are known for species within the allied Asian genus *Cycloneuroterus*, both are induced on the same host plant lineage (various *Cyclobalanopsis* species; Tang *et al*. 2011a, 2016a), as is typical of most other oak gallwasps. Of the 12 described Eastern Palearctic *Dryocosmus* species only one species, *D. kunugiphagus*, is known yet to have alternate sexual and asexual generations (Ide & Abe 2015). Hence further sampling on the appropriate host plants should reveal the alternate generations of other Asian *Dryocosmus* species and understand the peculiar pattern of alternate generations.

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7. **SUMMARY**

Cynipidae lies within the superfamily Cynipoidea of the Hymenoptera, which includes approximately 3000 described species (Fergusson 1995, Ronquist 1999). Cynipids are divided into two main trophic groups: the gall inducers, and the gall-associated inquilines. Recently, the higher-level taxonomy of Cynipidae has been changed, the family was divided into 12 monophyletic tribes from which 4 include inquilines (Ronquist *et al*. 2015).

The first part of our research focused on the inquiline cynipids, tribe Synergini sensu stricto, which attack hosts in the gallwasp tribe Cynipini (oak gallwasps). This tribe consits of seven genera, *Agastoroxenia*, *Saphonecrus*, *Synergus*, *Synophrus*, *Ufo*, *Lithosaphonecrus* and *Rhoophilus* (Bozsó *et al.* 2014, Ronquist *et al*. 2015, Schwéger *et al*. 2015a, b) of which *Synergus* and *Saphonecrus* were investigated in details. Our aim was to start to establish the phylogenetic relationships within the Synergini sensu stricto of which the necessary first step was to establish their morphotaxonomy, which included the description of new species of *Synergus* and *Saphonecrus* genera with the re-appraisal of all known EP *Synergus* and worldwide *Saphonecrus* species. New key to all EP *Synergus* species and to world known *Saphonecrus* species with the description of new species was given.

The phylogenetic analysis supported the monophyly of the large genus *Synergus* while the monophyly of *Saphonecrus* was rejected. However, recent studies revealed contradictions between the morphological discrimination and molecular phylogeny on species level, especially within both genera (Pénzes *et al*. 2009, Ács *et al.* 2010, Ronquist *et al*. 2015, Stone *et al.* 2002). All the newly described EP *Saphonecrus* and *Synergus* species are supported by distinct mitochondrial DNA haplotypes. On the other hand, some contradiction between morphology-based taxonomy and molecular phylogeny still remained considering the classification (Schwéger *et al*. 2015a, b).

Fifteen new species of *Saphonecrus* were described, *Saphonecrus chinensis* Tang & Schwéger, *S. gilvus* Melika & Schwéger, S. *globosus* Schwéger & Tang, *S. leleyi* Melika & Schwéger, *S. lithocarpii* Schwéger & Melika, *S. longinuxi* Schwéger & Melika, *S. morii* Schwéger & Tang, *S. nantoui* Tang, Schwéger & Melika, *S. nichollsi* Schwéger & Melika, *S. pachylomai* Schwéger, Tang & Melika, *S. robustus* Schwéger & Melika, *S. saliciniai* Melika, Tang & Schwéger, *S. shanzhukui* Melika & Tang, *S. symbioticus* Melika & Schwéger, and *S. taitungi* Schwéger, Tang & Melika, from the Eastern Palearctic. The status of earlier described species was re-evaluated. The current number of valid *Saphonecrus* species worldwide is raised to 36. Data on the diagnoses, biology, distribution, host galls and host plants of each species are given. The status of some earlier described *Saphonecrus* species was also discussed (Schwéger *et al.* 2015a). Morphology based delimitation completed our earlier molecular phylogenetic results (Bozsó *et al*. 2014, 2015) (Schwéger *et al.* 2015a, b). Host plant associations for the most of 36 *Saphonecrus* species are given also. 12 species develop on *Quercus* subgenus *Cyclobalanopsis*, 4 – 4 species on *Quercus* section Quercus and *Lithocarpus*, 5 species on *Quercus* section Cerris. In the Nearctic Region 2 species are known which associate with *Quercus* section Lobatae.

Eight new species of *Synergus* were described, *Synergus symbioticus* Schwéger & Melika, *S***.** *formosanus* Schwéger & Melika, *S. khazani* Melika & Schwéger, *S. abei* Melika & Schwéger, *S. belizinellus* Schwéger & Melika, *S. ishikarii* Melika & Schwéger, *S. changtitangi* Melika & Schwéger and *S. kawakamii* Tang & Melika, from the Eastern Palearctic. Descriptions, diagnoses, biology, and host associations for the new species and a key to all known Eastern Palearctic *Synergus* species are given. The discrimination of all taxa is supported by morphological and molecular data. We discussed the status of all previously described Eastern Palearctic *Synergus* species, and provided validation and synonymization of some species. Three *Saphonecrus* species were transferred to *Synergus*: *Synergus brevis* (Weld)**,** *Synergus hupingshanensis* **(**Liu, Yang & Zhu), and *Synergus yukawai* (Wachi, Ide & Abe)**.** The current phylogenetic and morphological examination of the Eastern Palearctic *Synergus* supported Ács *et al*. (2010)'s conclusion that palearctic *Synergus* comprise a monophyletic group, with Eastern Palearctic species nested among the Western Palearctic species. There is thus no evidence that Eastern and Western Palearctic *Synergus* species represent independent regional radiations. Of 14 Eastern Palearctic *Synergus* species for which the host gall and host plant associations are known, 11 species associate with hosts developing on *Quercus* subgenus *Quercus*. One species, *S. itoensis* is a gall-inducer on acorns of *Quercus* subgenus *Cyclobalanopsis*. Two *Synergus* species with opened or partially opened radial cell of the fore wing, *S. kawakamii* and *S. castaneus*, could not be placed reliably on the phylogenetic tree.

The second part of our work is focused on the gathering, pulling together all the fragmented data on the biology, ecology, phenology, life-cycles and taxonomic history of all Eastern Palearctic (EP) Cynipini (oak gallwasp) species (unpublished results). There are only few Cynipidae (Hymenoptera) reviews on the EP species (e.g. Dalla Torre & Kieffer 1910, Abe *et al*. 2007). Both are out of time, since then dozens of new species were described and a large number of nomenclatorial changes have been done. Nowadays, there is no faunistic review on EP Cynipini, all the data is fragmented, thus a compilation of a complete Cynipini (Cynipidae, Cynipoidea, Hymenoptera) annotated list for the EP (including few species known from the Oriental Region) is useful. The most completed annotated list for EP Cynipini, with a list of species with uncertain status is given.

8. ÖSSZEFOGLALÓ

A Cynipoidea családsorozaton belül, a gubacsdarazsak (Cynipidae) családjába mintegy 3000 leírt faj tartozik (Fergusson 1995, Ronquist 1999). A gubacsdarazsak két fő trofikai csoportra bonthatók: gubacsképzők és inkvilin gubacsdarazsak. A Cynipidae családon belül ma 12 monofiletikus tribust különítünk el, melyek közül 4 tribusban találhatóak inkvilinek (Ronquist és mtsai 2015).

Kutatásunk első nagy témaköre az inkvilin gubacsdarazsak, a Synergini sensu stricto tribus, mely fajok gazdái elsősorban a Cynipini tribusba sorolt tölgy gubacsdarazsak. Ezen belül 7 nem (genus) különíthető el, az *Agastoroxenia*, *Saphonecrus*, *Synergus*, *Synophrus*, *Ufo*, *Lithosaphonecrus és Rhoophilus* (Ronquist és mtsai 2015, Schwéger és mtsai 2015a, b), melyek közül a *Saphonecrus* és *Synergus* nemet vizsgáltuk részletesen. Munkánk során célunk volt a Synergini sensu stricto tribuson belüli filogenetikai kapcsolatok feltérképezése, melynek első fontos lépése a fajcsoportok morfotaxonómiai alapú elkülönítése volt, beleértve a *Synergus* és *Saphonecrus* nemen belüli új fajok leírását, valamint helyzetük újraértékelését, kiegészítve az eddig ismert összes *Saphonecrus* és összes kelet-palearktikus *Synergus* fajjal. Továbbá fontosnak tartottunk egy új, komplex és fajgazdag határozó kulcs megalkotását az eddig leírt kelet-palearktikus *Synergus* és összes *Saphonecrus* faj esetében az új fajok részletes leírásával kiegészítve.

A filogenetikai elemzés támogatja a fajgazdag *Synergus* nem monofiletikusságát, a *Saphonecrus* viszont nem monofiletikus (Pénzes és mtsai 2009, Ács és mtsai 2010, Ronquist és mtsai 2015, Stone és mtsai 2002). Azonban az újabb tanulmányok szerint ellentmondások vannak a faji szintű morfológiai alapú elkülönítés és a filogenetikai elemzés eredményének összevetése között, különös tekintettel az általunk vizsgált két nemre (Pénzes és mtsai 2009, Ács és mtsai 2010, Ronquist és mtsai 2015). Az összes leírt új Kelet-Palearktikus *Saphonecrus* és *Synergus* faj jól elkülönül a mitokondriális DNS haplotípusok alapján. Másrészről több a morfológiai alapú taxonómia és a molekuláris filogenetikai elemzés eredményei közötti bizonytalanság változatlanul fennáll (Schwéger és mtsai 2015a, b).

A *Saphonecrus* nem esetében tizenöt új fajt írtunk le a Kelet-Palearktikumban, melyek a következők: *Saphonecrus chinensis* Tang & Schwéger, *S. gilvus* Melika & Schwéger, S. *globosus* Schwéger & Tang, *S. leleyi* Melika & Schwéger, *S. lithocarpii* Schwéger & Melika, *S.*

longinuxi Schwéger & Melika, *S. morii* Schwéger & Tang, *S. nantoui* Tang, Schwéger & Melika, *S. nichollsi* Schwéger & Melika, *S. pachylomai* Schwéger, Tang & Melika, *S. robustus* Schwéger & Melika, *S. saliciniai* Melika, Tang & Schwéger, *S. shanzhukui* Melika & Tang, *S. symbioticus* Melika & Schwéger, éd *S. taitungi* Schwéger, Tang & Melika. A korábban leirt fajok értékelését, besorolását is elvégeztük. Jelenleg a *Saphonecrus* nemen belül 36 fajt ismerünk, részletesen tárgyaltam a fajok diagnózisát, elterjedését, gubacs- és növénygazda kapcsolatait, valamint a korábban leírt *Saphonecrus* fajokkal való összehasonlítását (Schwéger és mtsai 2015a). Korábbi molekuláris filogenetikai eredményeinket részletes morfológia alapú elkülönítéssel is kiegészítettük (Bozsó és mtsai 2014, 2015, Schwéger és mtsai 2015a, b). A legtöbb leírt *Saphonecrus* faj növénygazdája ismert. Közülük 12 faj a *Quercus* alnem *Cyclobalanopsis* fajain, 4 – 4 faj a *Quercus* alnem Quercus szekció fajain és *Lithocarpus* fajokon, 5 faj pedig a *Quercus* alnem Cerris szekció fajain található meg. A nearktikus régióban csak 2 fajnak ismert a növénygazdája, melyek a *Quercus* alnem Lobatae szekcióba tartozó tölgyek.

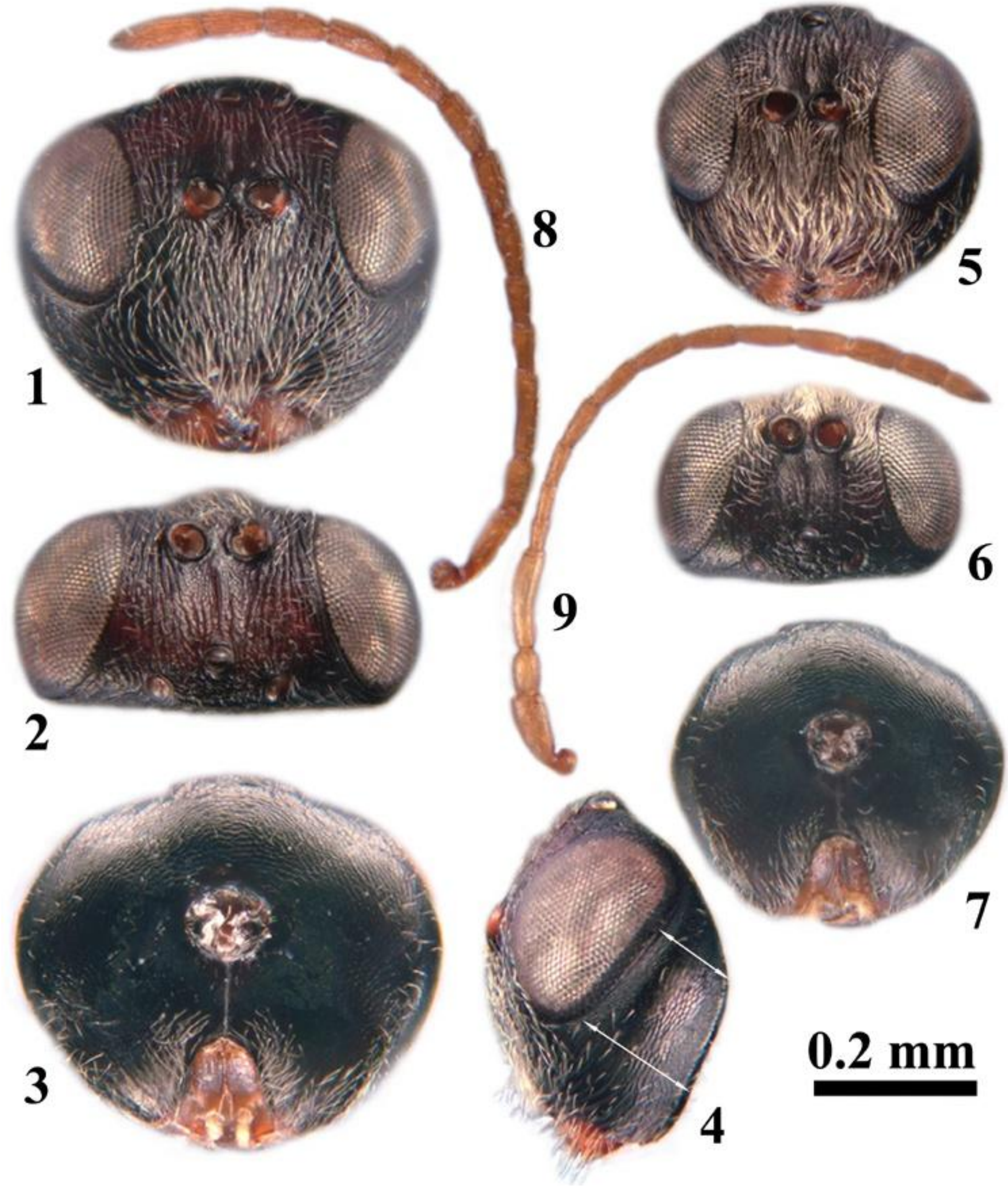
A *Synergus* nem esetében 8 új fajt írtunk le a Kelet-Palearktikumban, melyek a következők: *Synergus symbioticus* Schwéger & Melika, *S.* *formosanus* Schwéger & Melika, *S. khazani* Melika & Schwéger, *S. abei* Melika & Schwéger, *S. belizinellus* Schwéger & Melika, *S. ishikarii* Melika & Schwéger, *S. changtitangi* Melika & Schwéger és *S. kawakamii* Tang & Melika. Dolgozatomban tárgyaltam az új fajok leírását, diagnózisát, biológiáját, gubacs- és növénygazda kapcsolatait, valamint megalkottuk a Kelet-Palearktikus *Synergus* nem összes faját magába foglaló határozó kulcsát. Valamennyi tárgyalt taxon elkülönítését a molekuláris és morfológiai adataink egyaránt alátámasztották. vizsgáltuk a korábban leírt Kelet- Palearktikus *Synergus* fajok jelenlegi helyzetét, szinonimizációját az általunk leírt új fajokkal összevetve. A *Saphonecrus* nemből három faj került át a *Synergus* nembe, ezek a következők: *Synergus brevis* (Weld)**,** *Synergus hupingshanensis* **(**Liu, Yang & Zhu), és *Synergus yukawai* (Wachi, Ide & Abe). A Kelet-Palearktikus *Synergus* klád esetében a molekuláris és morfológiai vizsgálataink alátámasztják a korábban Ács és mtsai (2010) által kapott eredményeket, mely szerint a kelet és nyugat palearktikus *Synergus* együtt egy monofiletikus csoportot alkot. Nincs bizonyíték a Kelet- és Nyugat-Palearktikus *Synergus* fajok független regionális eredetére. A 14 eddig leírt Kelet-Palearktikus *Synergus* faj közül, melynek ismert a gubacs- és növénygazdája is, 11 faj a *Quercus* alnem Quercus tölgy szekció fajain találhatóak meg. Egy faj, a *S. itoensis*, a *Quercus* (*Cyclobalanopsis*) alnembe tartozó tölgyek makkjaiban képez gubacsot. A *Synergus* két tagját, *a*

S. kawakamii és a *S. castaneus* fajokat, melyek elülső szárnyán lévő radiális sejt részben vagy teljesen nyitott, nem tudtuk egyértelműen elhelyezni a génfán.

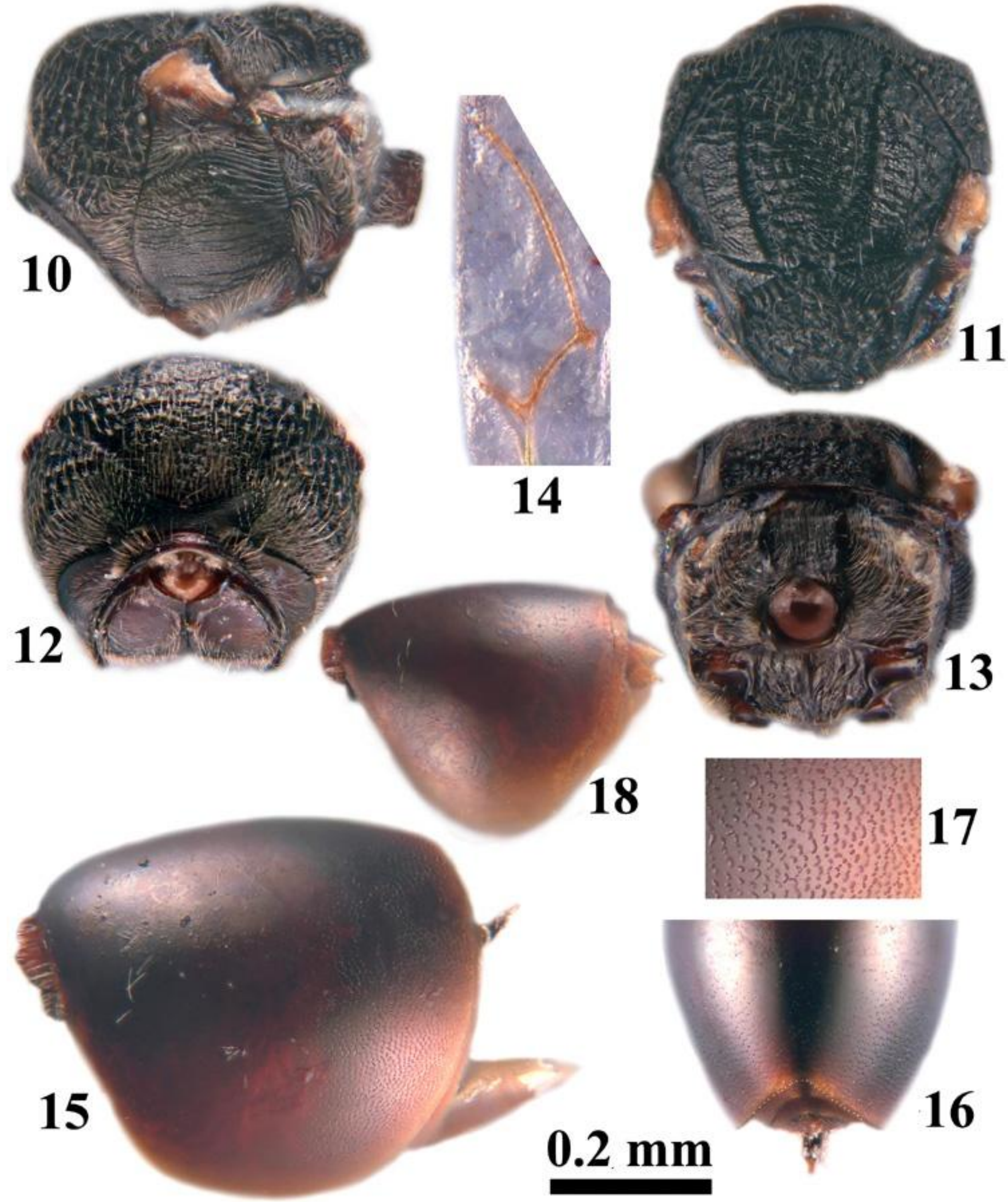
A munkánk második fő témája a Kelet-Palearktikus Cynipini (tölgy gubacsdarázs) tribusba tartozó fajok biológiájának, ökológiájának, fenológiájának, életciklusainak, és taxonómiai történetüknek összegzése (leközlés alatt álló eredmények), mely adatok számos kis közleményben voltak fellelhetőek. Jelenleg néhány összefoglaló dolgozat áll rendelkezésünkre a Kelet-Palearktikumban elterjedt Cynipidae fajokról (pl. Dalla Torre & Kieffer 1910, Abe és mtsai 2007). Ezek közül a művek közül a legtöbb elavult az azóta leírt új fajok és a nevezéktan gyakori és gyors változása miatt. Így hasznosnak bizonyult egy összegző lista létrehozása a Kelet-Palearktikus Cynipini (Cynipoidea, Hymenoptera) tribus jelenleg leírt fajairól (belevéve a néhány Orientális Régióból ismert fajt is). A Kelet-Palearktikus Cynipini tribus részletes listája kiegészítve a bizonytalan státuszú fajokkal a dolgozat függelékének 9.2. és 9.3. részében található (leközlés alatt álló eredmények).

9. APPENDICES

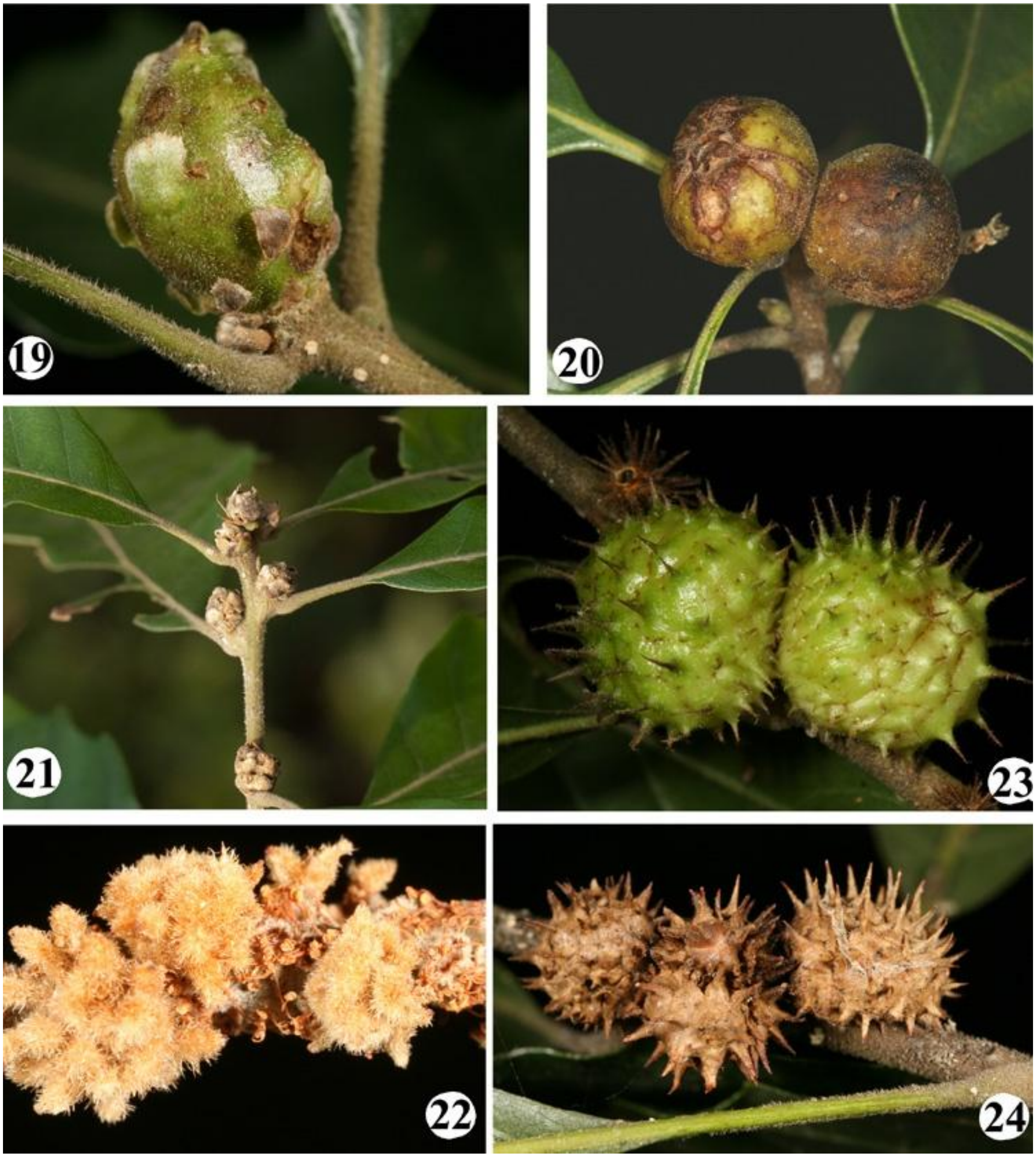
9.1. Morphological peculiarities and hosts of *Lithosaphonecrus, Rhoophilus, Synophrus, Ufo, Saphonecrus* and *Synergus*



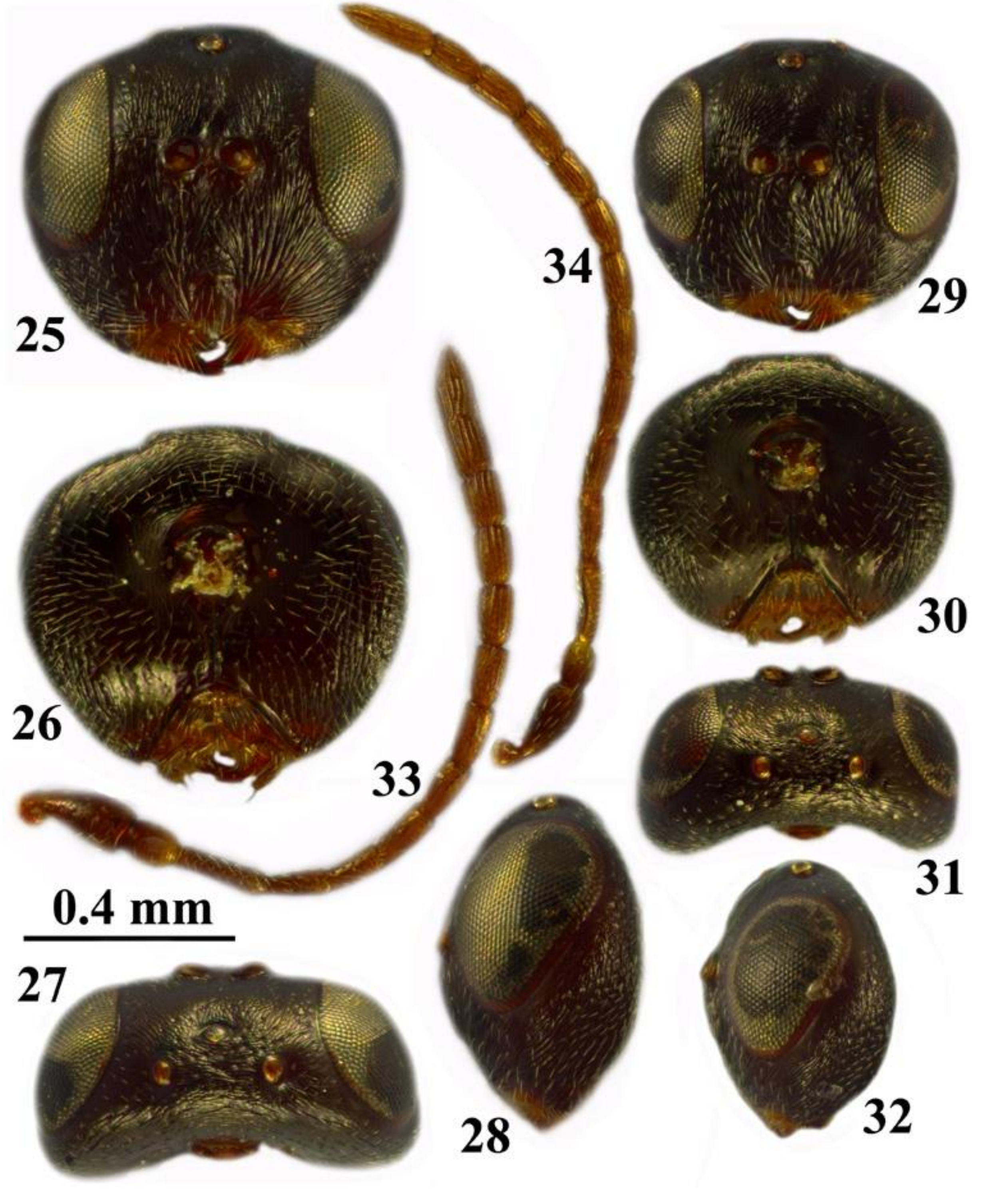
FIGURES A1–A9. *Lithosaphonecrus dakengi*: 1–4, head, female: 1, frontal view, 2, dorsal view, 3, posterior view, 4, lateral view. 5–7, head, male: 5, frontal view, 6, dorsal view, 7, posterior view. 8–9, antenna: 8, female, 9, male.



FIGURES A10–A18. *Lithosaphonecrus dakengi*: 10–17, female: 10, mesosoma, lateral view, 11, mesosoma, dorsal view, 12, mesosoma, frontal view, 13, metascutellum and propodeum, posterodorsal view, 14, fore wing, part, 15, metasoma, lateral view, 16, metasoma, posterior part, dorsal view, 17, surface sculpture of posterior end of metasomal tergite 2+3, part. 18, metasoma, male, lateral view.

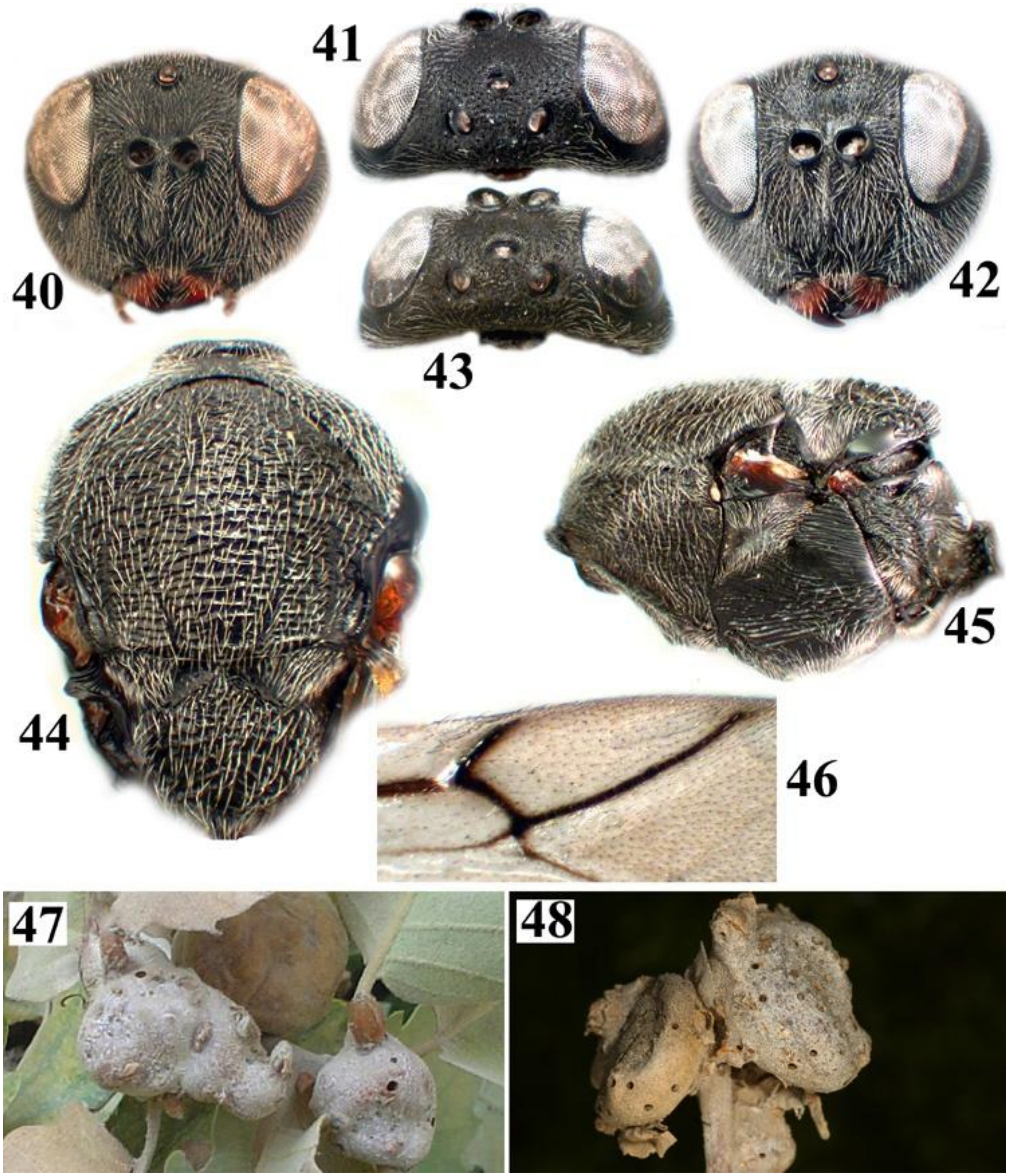


FIGURES A19–A24. Host galls of *Lithosaphonecrus* spp.: 19, undescribed bud gall, 20, undescribed bud gall, 21, undescribed bud gall, 22, undescribed catkin gall, 23–24, a sea-urchin-like detachable stem gall on twigs: 23, young growing galls, 24, mature galls (photos by G. Csóka and C.-T. Tang).

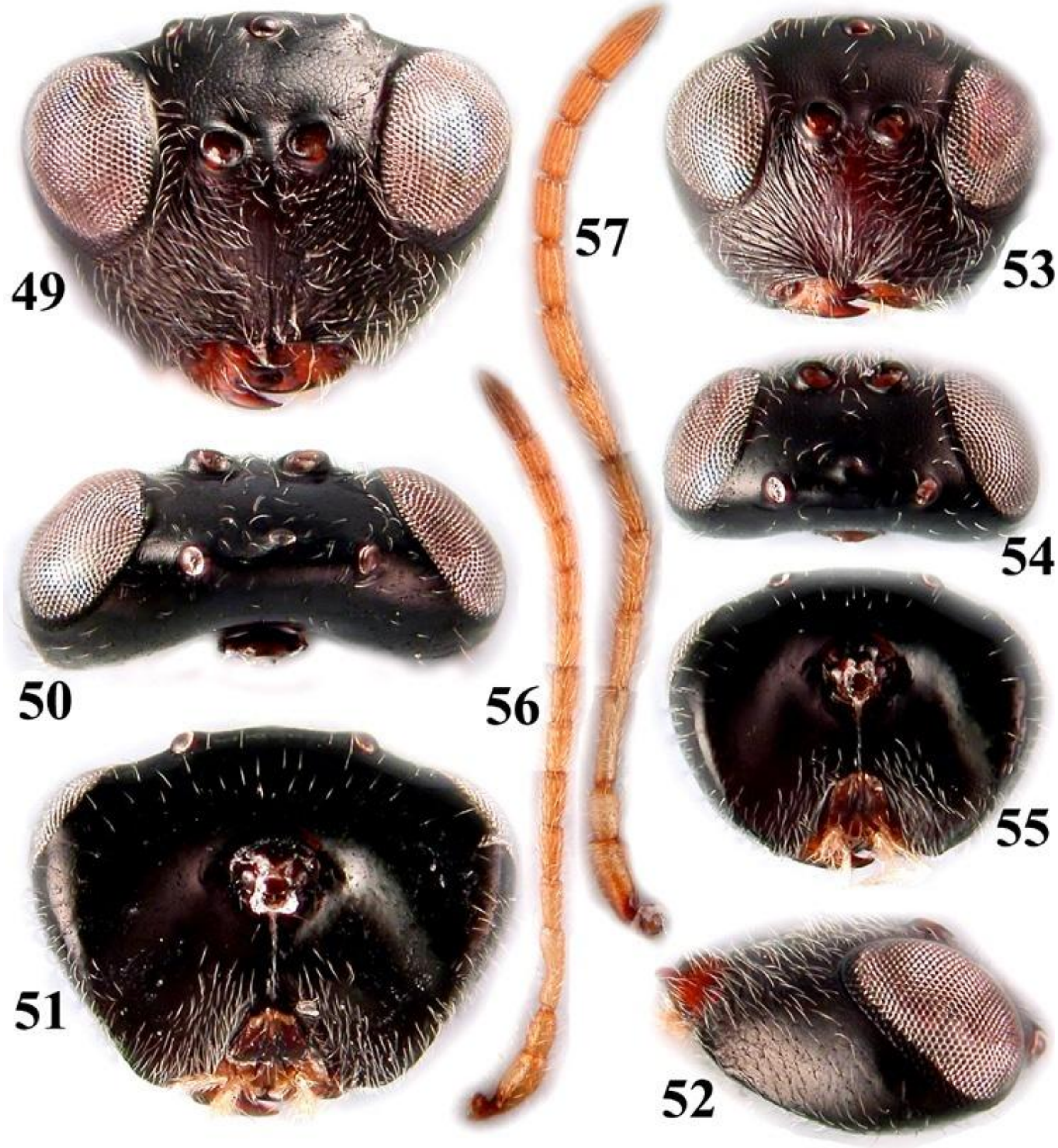


FIGURES A25–A34. *Rhoophilus loewi*: 25–28, head, female: 25, frontal view, 26, posterior view, 27, dorsal view, 28, lateral view. 29–32, head, male: 29, frontal view, 30, posterior view, 31, dorsal view, 32, lateral view. 33–34, antenna: 33, female, 34, male.

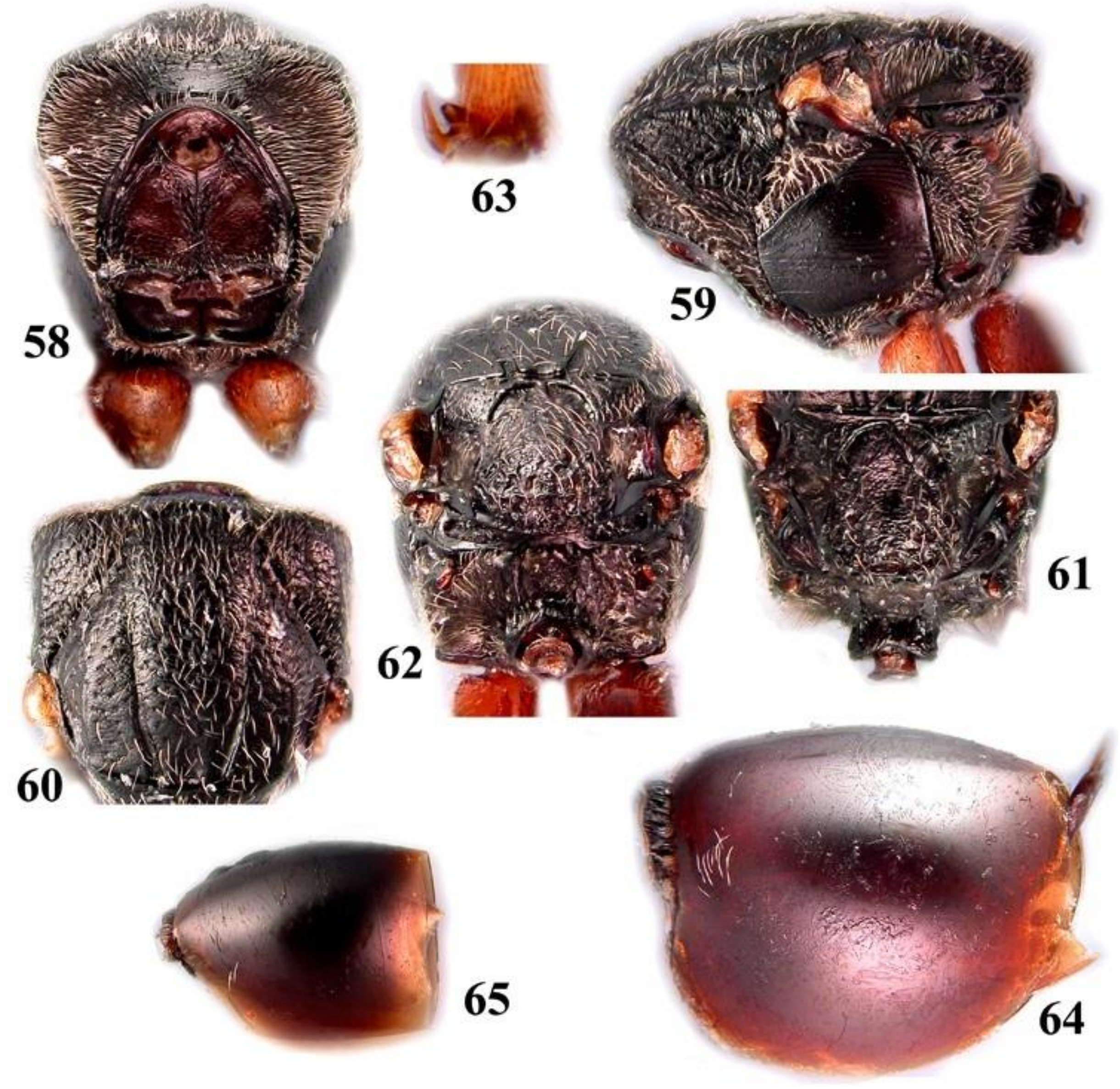
FIGURES A35–A39. *Rhoophilus loewi*, female: 35, mesosoma, anterodorsal view, 36, mesosoma, posterodorsal view, 37, mesosoma, lateral view, 38, metascutellum and propodeum, posterodorsal view, 39, metasoma, lateral view.



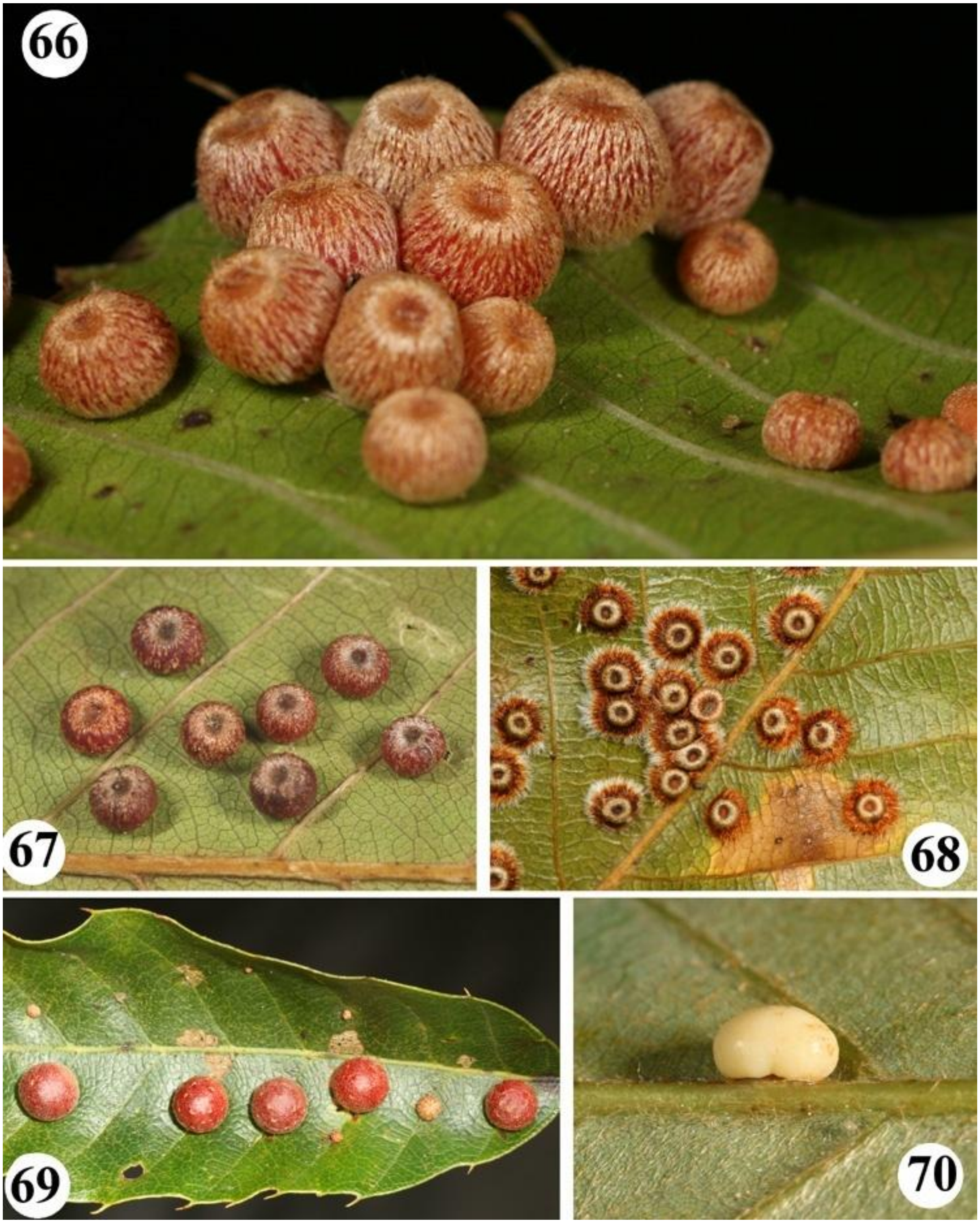
FIGURES A40–A48. *Synophrus olivieri*: 40–41, head, female: 40, frontal view, 41, dorsal view, 42–43, head, male: 42, frontal view, 43, dorsal view. 44–46, female: 44, mesosoma, dorsal view, 45, mesosoma, lateral view, 46, fore wing, part. 47–48, gall (photos by M. Tavakoli).



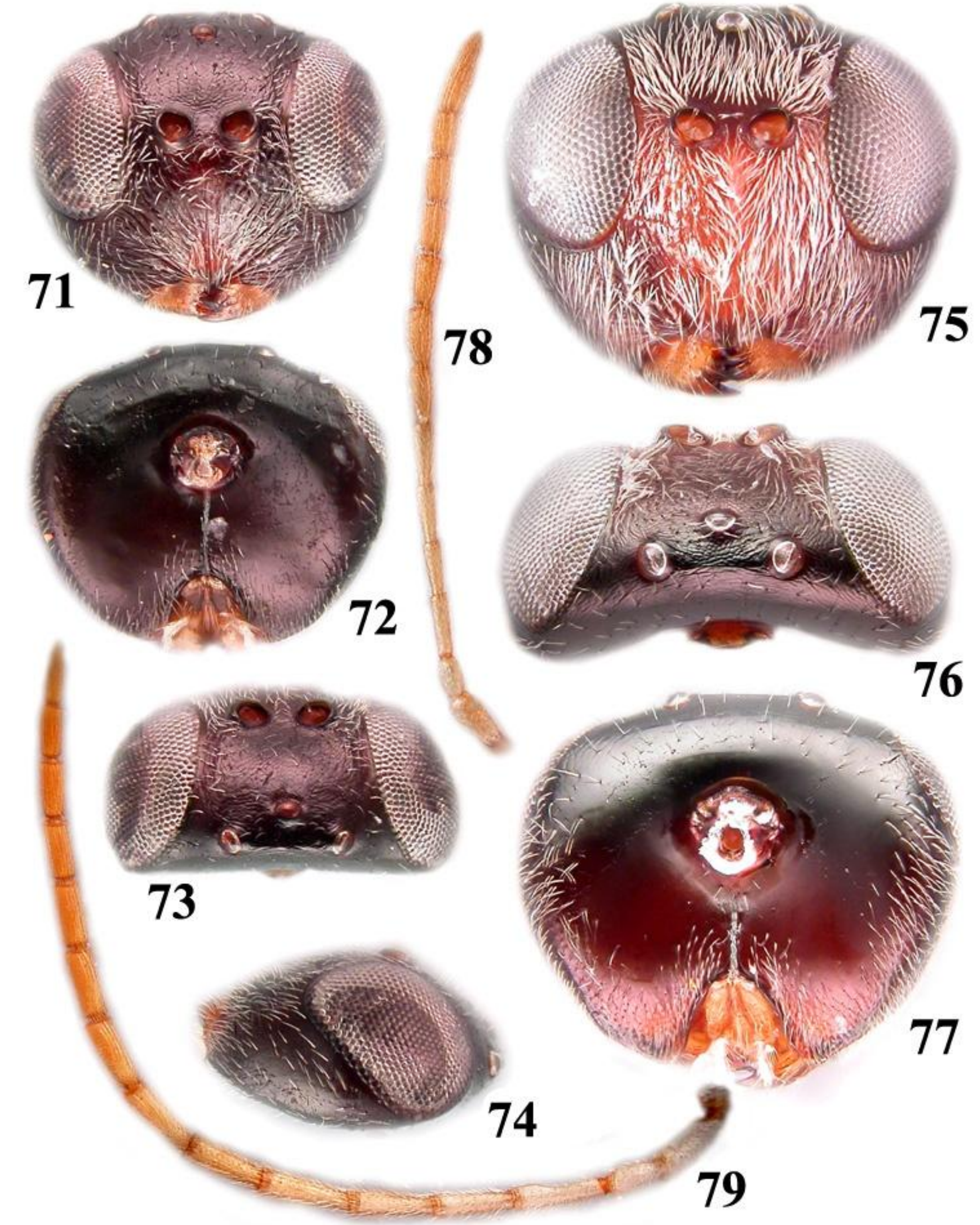
FIGURES A49–A57. *Ufo cerroneuroteri*: 49–52, head, female: 49, frontal view, 50, dorsal view, 51, posterior view, 52, lateral view. 53–55, head, male: 53, frontal view, 54, dorsal view, 55, posterior view. 56–57, antenna: 56, female, 57, male.



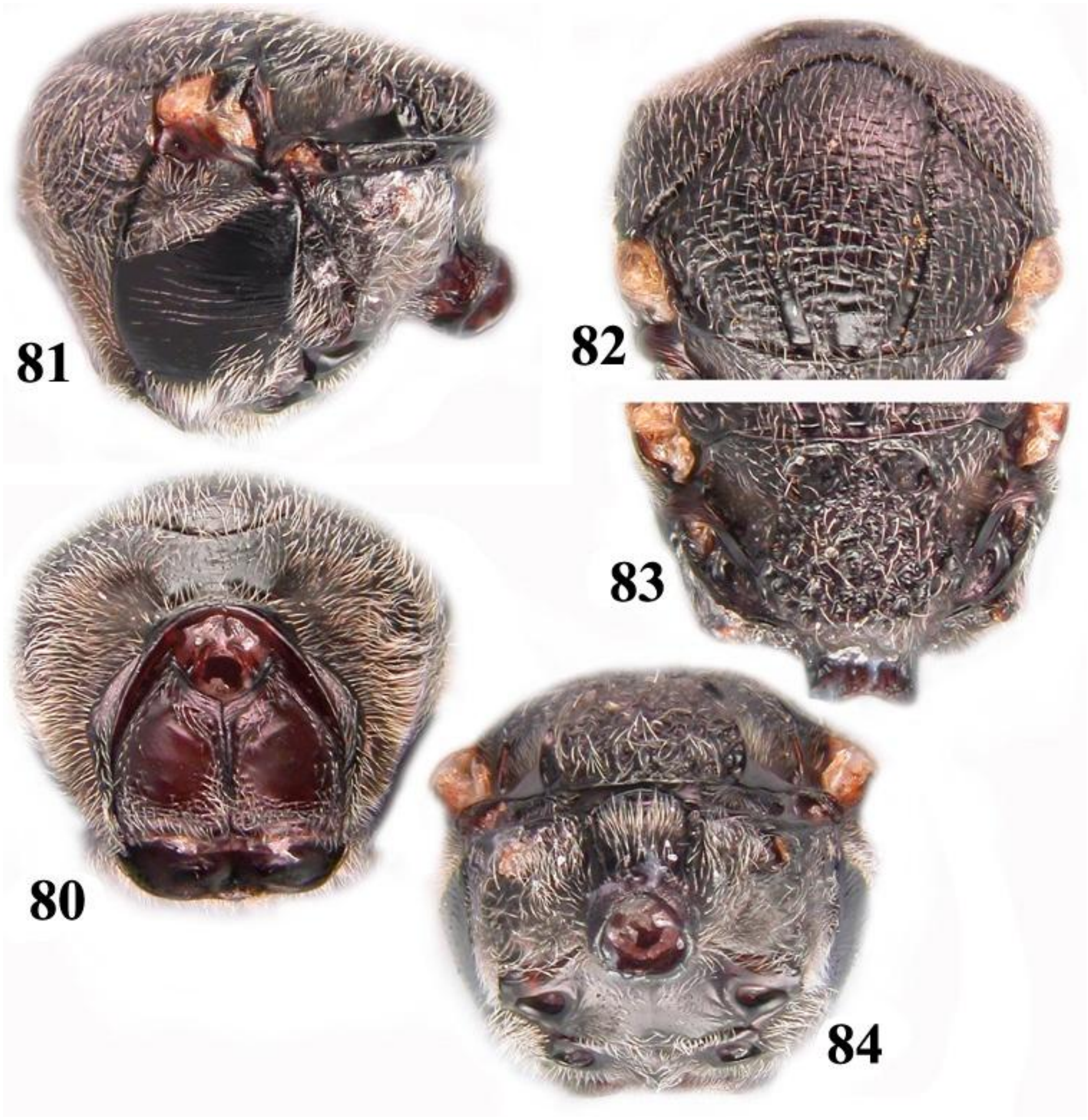
FIGURES A58–A65. *Ufo cerroneuroteri*: 58–66, female: 10, pronotum and propleuron, anterior view, 11, mesosoma, lateral view, 12, mesoscutum, dorsal view, 13, mesoscutellum, dorsal view, 14, metascutellum and propodeum, posterodorsal view, 15, tarsal claw, 16, metasoma, female, lateral view. 17, metasoma, male, lateral view.



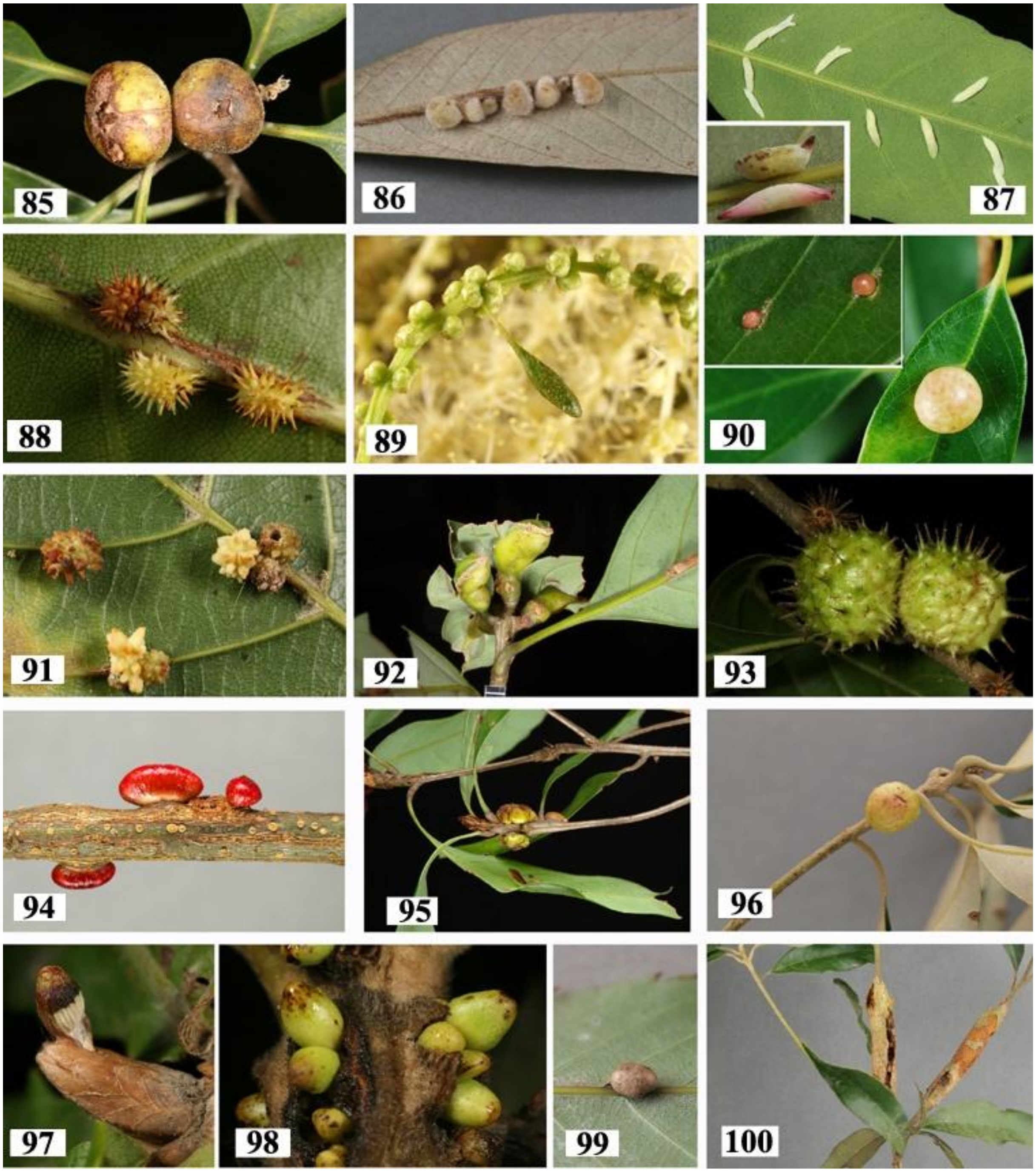
FIGURES A66–A70. Host oak galls of *Ufo* spp.: 66, *Cerroneuroterus vonkuenburgi*, asexual galls, 67, *C. monzeni*, asexual galls, 68, *Latuspina nawai*, asexual galls, 69, *Trichagalma acutissimae*, asexual galls, 70, *Neuroterus hakonensis* (= *Andricus kunugifoliae*), asexual galls (photos by G. Csóka).



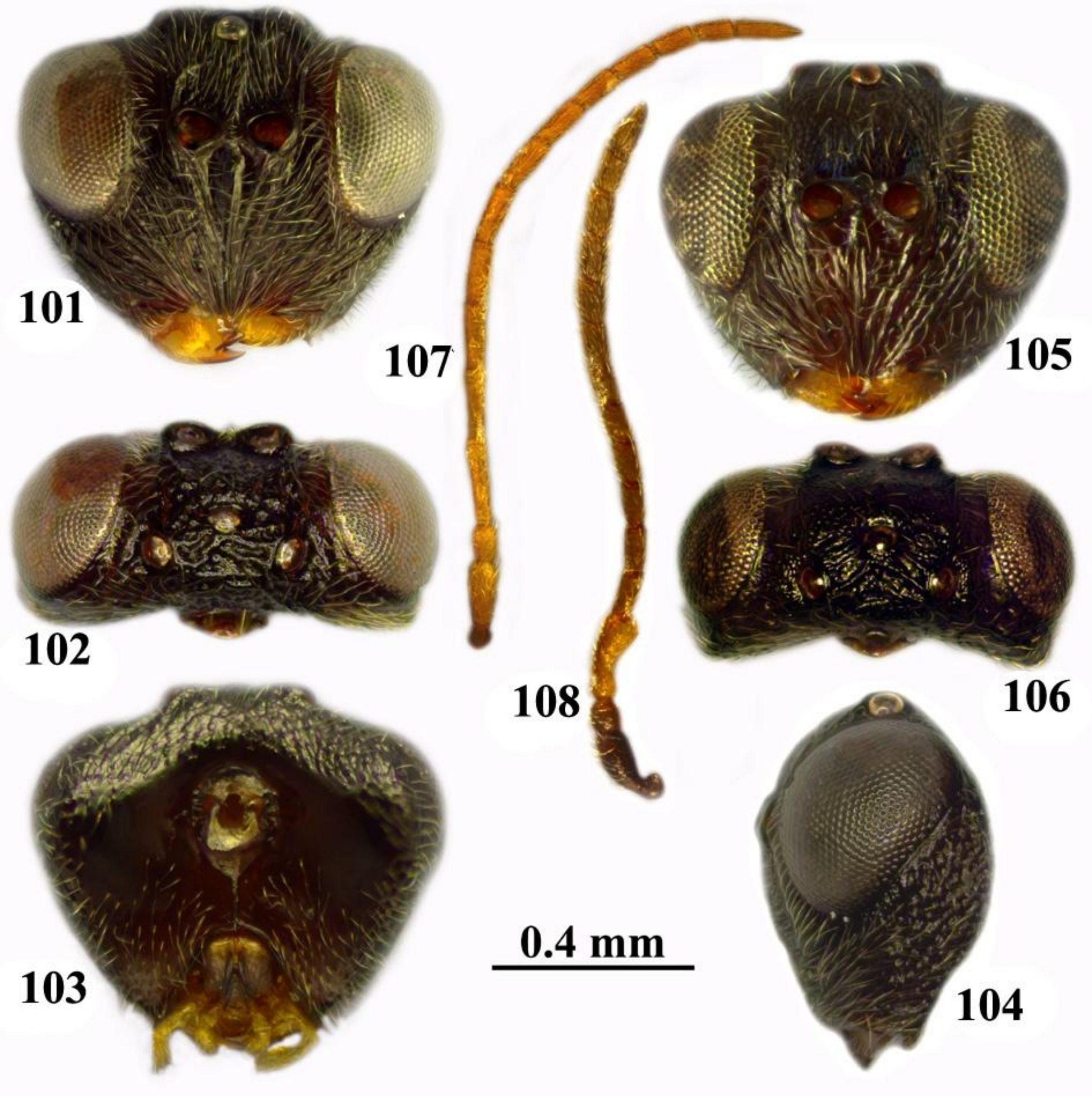
FIGURES A71–79. *Saphonecrus lithocarpii*: 71–74, head, female: 71, frontal view, 72, posterior view, 73, dorsal view, 74, lateral view. 75–77, head, male: 75, frontal view, 76, dorsal view, 77, posterior view. 78–79, antenna: 78, female, 79, male.



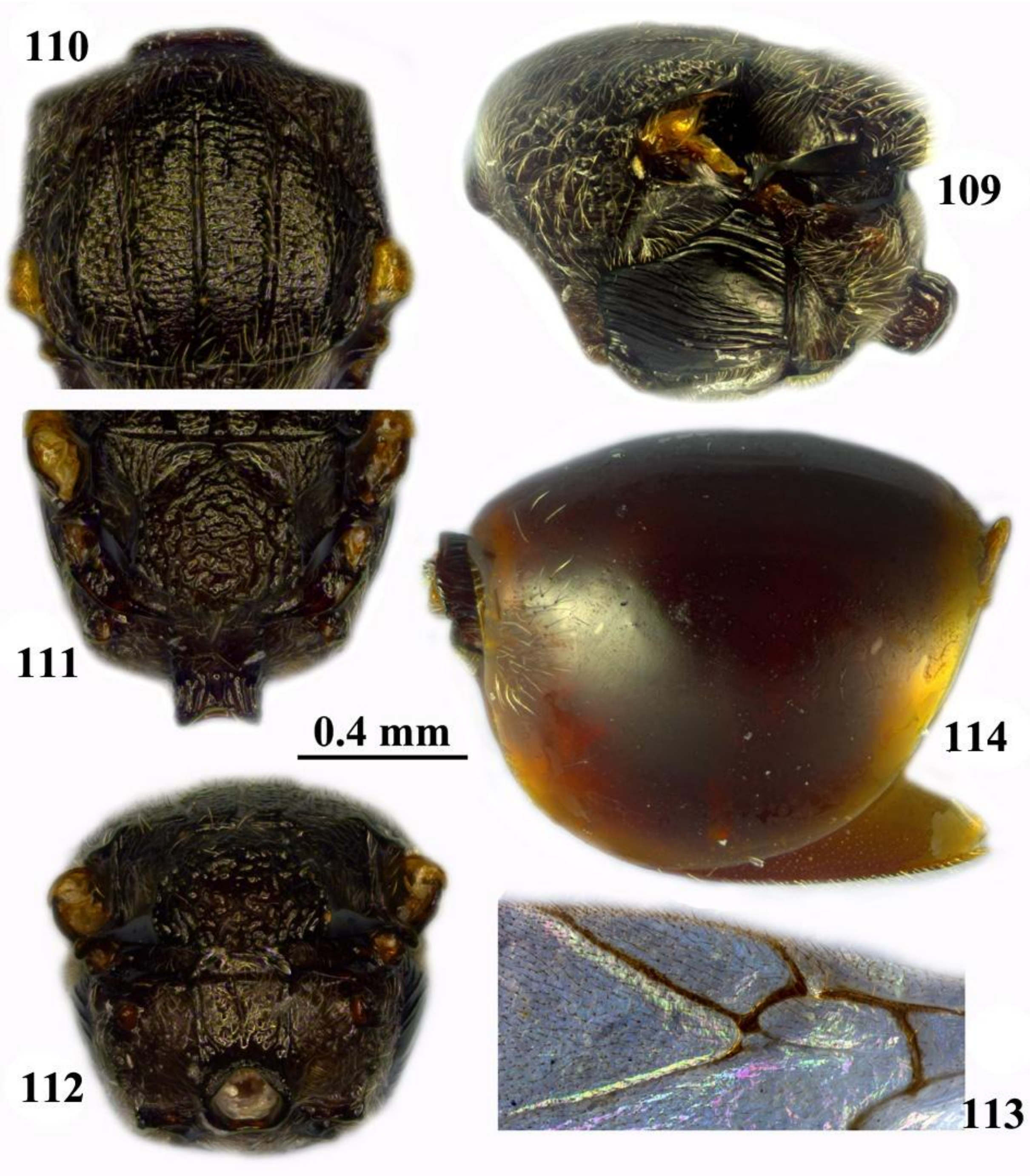
FIGURES A80–84. *Saphonecrus lithocarpii*, female: 80, pronotum and propleuron, anterior view, 81, mesosoma, lateral view, 82, mesoscutum, dorsal view, 83, mesoscutellum, dorsal view, 84, metascutellum and propodeum, posterodorsal view.



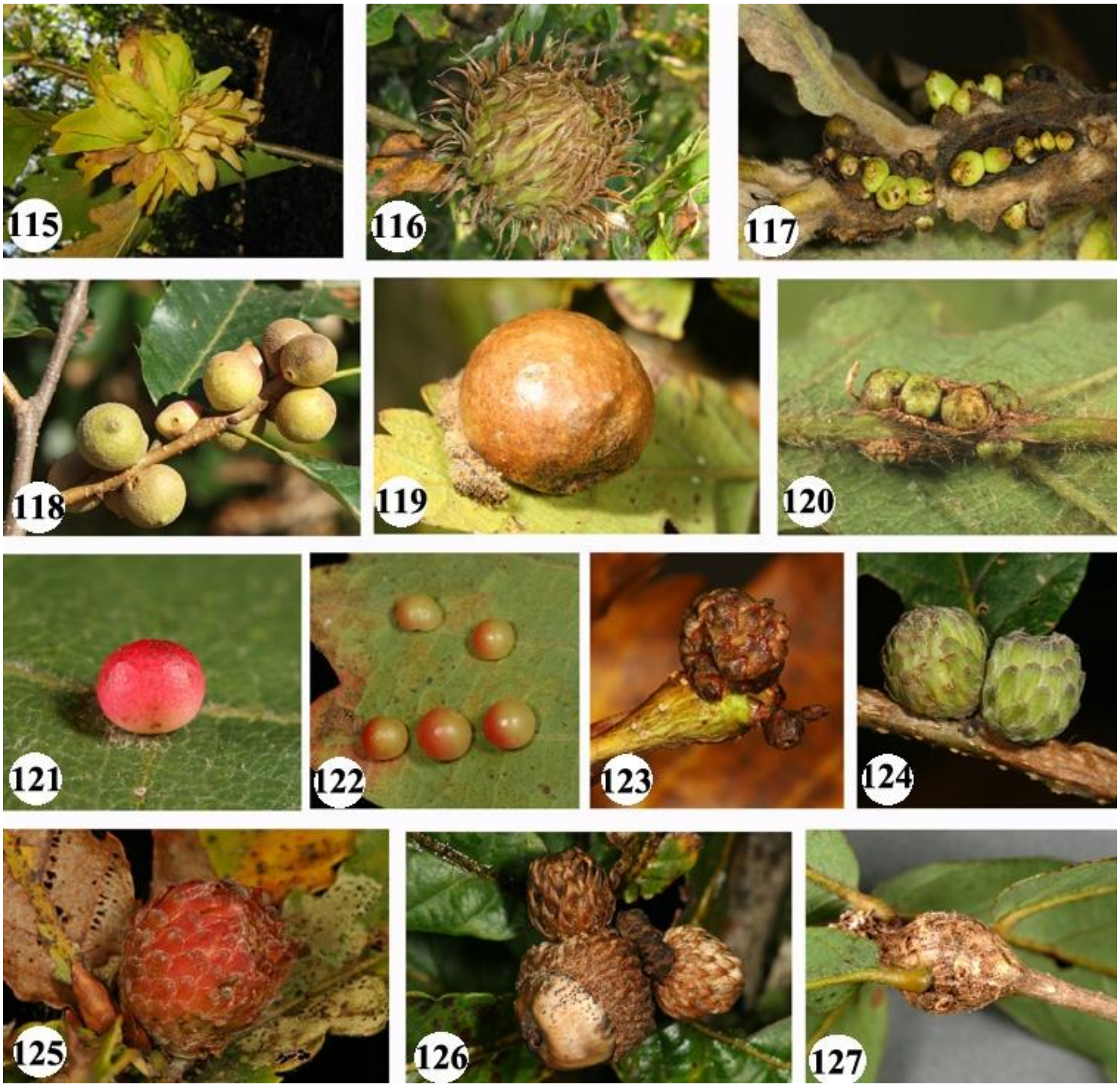
FIGURES A85–A100. Host galls of newly described *Saphonecrus* spp.: 85, undescribed bud gall, 86, undescribed leaf gall, 87, undescribed leaf gall, 88, undescribed leaf gall, 89, undescribed catkin gall, 90, undescribed leaf gall, 91, undescribed leaf gall, 92, undescribed leaf petiole thickening gall, 93, undescribed stem swelling-like gall, 94, undescribed stem swelling-like gall on *Q. longinuxi*, 95, undescribed stem swelling-like gall on *Q. pachylomai*, 96, undescribed rounded stem swelling-like gall, 97, undescribed bud gall, 98, asexual gall of *Andricus hakonensis* (=*A.symbioticus*), 99, undescribed egg-shaped gall on leaf midrib, 100, undescribed *Dryocosmus* multilocular stem swelling-like gall.



FIGURES A101–108. *Synergus belizinellus*: 101–104, head, female: 101, frontal view, 102, dorsal view, 103, posterior view, 104, lateral view, 105–106, head, male: 105, frontal view, 106, dorsal view. 107–108, antenna: 107, female, 108, male.



FIGURES A109–A114. *Synergus belizinellus*, female: 109, mesosoma, lateral view, 110, mesoscutum, dorsal view, 111, mesoscutellum, dorsal view, 112, metascutellum and propodeum, posterodorsal view, 113, fore wing, part, 114, metasoma, lateral view.



FIGURES A115–A127. Host oak galls of newly described *Synergus* spp.: 115, *Andricus kashiwaphilus*, asexual gall, 116, *A. mukaigawae*, asexual gall, 117, *A. hakonensis* (=*A. symbioticus*), asexual galls, 118, *Trichagalma formosana*, asexual galls, 119, *Belizinella* sp., asexual gall, 120, *Ussuraspis* sp., asexual gall, 121, unknown leaf gall, 122, unknown leaf gall, 123, unknown acorn gall, 124, unknown bud gall, 125, unknown bud gall, 126, unknown acorn gall (photos by G. Csóka). 127, unknown stem swelling-like gall (photos by Chang Ti Tang).

9. 2. Annotated list of Cynipini of the Eastern Palearctic (Cynipoidea: Cynipidae)

There are only few Cynipidae (Hymenoptera) reviews on the Eastern Palearctic species (Dalla Torre & Kieffer 1910, Abe *et al*. 2007). Both are out of time and since then dozens of new species were described and a large number of nomenclatorial changes have been done. Recently some review papers were published on the Eastern Palearctic cynipid inquilines (Cynipidae: Synergini) (Pénzes *et al.* 2012) and its genera: *Lithosaphonecrus* Tang, Melika & Bozsó (Bozsó *et al*. 2015), *Saphonecrus* Dalla Torre & Kieffer (Schwéger *et al.* 2015b), *Synergus* Hartig (Schwéger *et al*. 2015b), and *Ufo* Melika & Pujade-Villar (Melika *et al*. 2012). Abe *et al*. (2007) listed all the known Eastern Palearctic rose gallwasps (Diplolepidini) and herb gall wasps ("Aylacini"), while the list of oak gallwasps (Cynipini) currently is far from completeness.

Oak cynipid biology is in a period of rapid advance, both in terms of our understanding of cynipid biology and of resolution of taxonomic issues within the Cynipini. New genera, species and generations continue to be discovered in Japan (Ide *et al*. 2010, 2012, 2013, 2016, Wachi & Abe 2010), Taiwan (Melika *et al*. 2010, 2011, 2012, 2013, Tang *et al*. 2009, 2011a, b, 2012a, b, 2016a, b, c), China (Pujade-Villar & Wang 2012, Wang *et al*. 2013a, b, Abe *et al*. 2014a, Pujade-Villar *et al*. 2014), Vietnam (Abe *et al.* 2014b). In particular, Taiwan and China are areas with high oak (*Quercus* L.) and oak relatives' (*Castanea* Miller, *Castanopsis* Miller, *Lithocarpus* Blume) species richness whose cynipid faunas remain little-studied, and future work will certainly reveal further new species.

This list summarizes what is known of the biology and taxonomic history of each oak gallwasp species and generation. We have had to address two difficult issues – the set of recognized species and lifecycles (discussed further below), and the sources of information used. The information is drawn from our own surveys and from selected published literature. Literature sources are given where appropriate, but we have not attempted to provide exhaustive literature support for data on common and widespread species. Where possible we cite regional reviews (e.g. Kovalev (1965) for Far East Russia, Monzen (1953, 1954) for Japan). The Eastern Palearctic as here defined includes Asia east to Iran, the Ciscaucasus (Transcaucasus) and the Ural Mountains. Species known only from more western regions, such as from Iran, the Transcaucasus, Dagestan are not included.

Genera and species are given in alphabetical order.

Andricus Hartig, 1840

Andricus deqingis Wang, Guo & Chen, 2013

Lifecycle. Only the sexual generation is known (Wang, Guo & Chen 2013).
Geographic distribution. China: Zhejiang (Wang, Guo & Chen 2013).
Host plants. *Quercus* sp. (Wang, Guo & Chen 2013).
Gall location and structure. Galls on branches and twigs, 1.0–2.5 mm long, yellowish, usually in clusters, each gall contains single thin-walled larval chamber (Wang, Guo & Chen 2013).
Phenology. Adults emerge in May (Wang, Guo & Chen 2013).

Andricus flavus Pujade-Villar, Wang, Guo & Chen, 2014

Lifecycle. Only the sexual generation is known (Pujade-Villar *et al*. 2014).
Geographic distribution. China: Zhejiang (Pujade-Villar *et al.* 2014).
Host plants. *Quercus fabrei* Hance (Pujade-Villar *et al*. 2014).

Gall location and structure. Multilocular leaf galls. Individual galls are nearly spherical, usually solely located on the underside of leaves. The young gall is juicy and freshly green, the surface is covered with small raised tubercles. The gall is brown or grey with a tough woody wall, 2.0–3.0 mm in diameter; turns dry and dark brown when mature, contains 4–5 larval chambers, each 0.5–0.7 mm in diameter (Pujade-Villar *et al*. 2014) .

Phenology. Galls appear on the host plant from early April; mature in early May; adults emerge in late May (Pujade-Villar *et al*. 2014).

Similar galls. The galls somehow resembles those of *Andricus xishuangbannaus* (Tang *et al*. 2012b) and *A. pseudocurvator* (Tang *et al*. 2011b).

Andricus formosanus Tang & Melika, 2009

Lifecycle. Only the sexual generation is known (Tang *et al*. 2009).

Geographic distribution. Taiwan (Pingtung County), the only natural stands of *Q. dentata* in Taiwan (Lu *et al*. 2006). It is possible that this species also occurs in continental China, as well as in Japan and the Russian Far East, where *Q. dentata* is a common species.

Host plants. *Quercus dentata* Thunb. (Tang *et al*. 2009).

Gall location and structure. Aggregated integral leaf galls cause swelling on both, upper and lower surfaces of the leaf. Individual galls are approximately spherical, 3.5–5.0 mm in height, each contains a single (unilocular) thin-walled larval chamber, 1.5–1.7 mm in diameter, attached by a tiny filament to the outer wall of the gall. In mature galls, the larval chamber loses its connection to the gall wall, and rolls freely within an internal air space. Though galls can occur separately on a leaf, they are often aggregated into masses 20–70 mm long that distort the leaf blade. Young galls are fleshy and pale green to yellowish, remaining soft when mature (Figs A128–129) (Tang *et al*. 2009).

Phenology. Galls mature in March; adults emerge in late March (Tang *et al*. 2009).

Similar galls. *Andricus formosanus* most closely resembles the sexual generation of an Eastern Palearctic species, *Andricus moriokae* Monzen which induces integral leaf galls on *Q. dentata* and *Q. serrata* Thunb. (= *Q. glandulifera* Blume) and is known from Japan and the Russian Far East (Monzen 1953, Kovalev 1965). Although the galls induced by the two species are structurally similar, in *A. formosanus* the gall clusters always much bigger, comprising many galls, often merged together, while in *A. moriokae* only a few galls are typically found on each leaf.

Andricus hakonensis (Ashmead, 1904)

Synonyms: *Callirhytis hakonensis* Ashmead, 1904; *Andricus attractus* Kovalev, 1965 (Wachi & Abe 2010); *Andricus symbioticus* Kovalev, 1965 (Wachi & Abe 2010); *Andricus oblongus* Monzen, 1953 (Yukawa & Masuda 1996). *Andricus hakonensis* (Ashmead, 1904) comb. nova in Wachi & Abe (2010).

Lifecycle. Alternating sexual and asexual generations are known (Wachi & Abe 2010).

Geographic distribution. Japan (Hokkaido, Honshu, Shikoku, Kyushu), Russian Far East (Lake Khasan in Primorie), Korea (Kovalev 1965, Yukawa & Masuda 1996, Katsuda & Yukawa 2004, Abe 1988, 1992, Wachi & Abe 2010).

Host plants. *Quercus aliena* Blume, *Q. dentata, Q. mongolica* Fisch. ex Ledeb., *Q. serrata* (Kovalev 1965, Abe 1992, Katsuda & Yukawa 2004).

Gall location and structure. Asexual generation bark galls are rounded-oblong, smooth, 7–8 mm high; green or greenish-raspberry, usually clustered on twig with a single larval cell (Fig.

A98, A117). The gall is secreting honeydew-like sticky substance which attracts ants and protect galls against parasitoid attack (Kovalev 1965, Abe 1988, 1992). Sexual generation galls are irregular spherical swelling of leaf vein and petiole; the immature gall is partially red, the mature one is yellowish green to green; with several, ovoid larval cells in the gall (Fig. A130) (Wachi & Abe 2010).

Phenology. The female adult of the asexual generation oviposits into buds before the bud burst, in early spring. The gall of the sexual generation appears on the leaf petiole or midrib in spring; adults emerge in early summer. Asexual galls appear on the twigs in late summer to autumn; adults emerge in early spring of the following year or even one year later (Yukawa & Masuda 1996).

Similar galls. The asexual generation galls are similar to those of the asexual generation of the western-palearctic species *Andricus sieboldi* (Hartig, 1843) [erroneously mentioned by Kovalev (1965) as *A. testaceipes* Hartig, 1840]. However, in contrast to *A. sieboldi*, the growing asexual galls of *A. hakonensis* produce honeydew and attract ants; galls fall when they mature, in late summer (Kovalev 1965). Asexual galls cluster encircling young sprouts, and are very similar to those of the asexual generation of western-palearctic *Dryocosmus cerriphilus* Giraud, 1859, which also produce honeydew and attract ants (Abe 1988, 1992).

Comments. *Andricus oblongus* Monzen, 1953 was described based on females only, which induce gall masses on the bark of *Q. serrata* in Japan (Monzen 1953). In the Monzen collection (Kyoto University) 11 pins with adults were found, all of which belong to an inquiline *Synergus* species; also the original description is a *Synergus* description (Monzen (1953). Thus, the name cannot be used for a gallwasp. According Yukawa & Masuda (1996) what Monzen (1953) described as *A. oblongus* is an *Andricus symbioticus* gall attacked by inquilines.

Andricus kashiwaphilus Abe, 1998

Lifecycle. Alternating sexual and asexual generations are known (Abe 1998).

Geographical distribution. Japan (Hokkaido, Chugoku, Kyushu) (Abe 1998), Russian Far East (Schwéger *et al*. 2015a, b), China (Pujade-Villar *et al.* 2016).

Host plants. *Quercus dentata* (Abe *et al.* 1998, 2007, Melika 2012).

Gall location and structure. The flower-shaped asexual gall is single or sometimes a few galls clustered, in shape similar to flower of rose, surrounded by compact leaf clusters, developed from axillary bud; the single larval cell is oval, 3.5–4.0 mm in diameter and 6.0 mm high (Fig. A115). Sexual galls are integral leaf galls, usually located on the leaf midrib (Abe 1998).

Phenology. Life cycle is very similar to that of *A. mukaigawae* (Wachi *et al*. 2012).

Comments. The morphology of adults similar to that of *A. mukaigawae* and thus it is complicate to differentiate the two species based on their morphology only (Abe *et al*. 2007).

Andricus marmoratus Kovalev, 1965

Lifecycle. Only the sexual generation is known (Kovalev 1965).

Geographic distribution. Russian Far East (Kovalev 1965).

Host plants. *Quercus mongolica* (Kovalev 1965, Melika 2012).

Gall location and structure. Tiny unilocular integral spherical leaf galls, 1–2 mm in diameter; green when growing, turn brown when mature (Kovalev 1965).

Phenology. Adults emerge in May (Kovalev 1965).

Comments. This species is closely resembles *A. moriokae* (Kovalev 1965, Abe *et al*. 2007).

***Andricus mairei* (Kieffer, 1906)**

Synonyms: Originally was described in *Parandricus* Kieffer, 1906, a genus synonymized to *Andricus* (Melika & Abrahamson 2002).

Lifecycle. Only the sexual generation is known (Kieffer 1906).

Geographic distribution. China (Hunan Province) (Kieffer 1906, Yang *et al*. 2012).

Host plants. *Quercus serrata* (= *Q. glandulifera* var. *brevipetiolata* Nakai) (Yang *et al*. 2012).

Gall location and structure. Catkin galls that forms clusters of up to 30 galls in one catkin (Abe *et al.* 2007, Yang *et al*. 2012).

***Andricus mesostegius* Kovalev, 1965**

Lifecycle. Only the sexual generation is known. The species was described on the basis of males only (Kovalev 1965).

Geographic distribution. Russia (Far East) (Kovalev 1965, Melika 2012).

Host plants. *Quercus dentata* (Kovalev 1965).

Gall location and structure. The gall is unknown; probably inconspicuous bud galls (Melika 2012).

***Andricus moriokae* Monzen, 1953**

Lifecycle. Alternating sexual and asexual generations are known. The sexual generation was described by Monzen (1953) while the asexual generation was found later (Katsuda & Yukawa 2003, Abe *et al.* 2007).

Geographic distribution. Japan and Russia (Far East) (Monzen 1953, Kovalev 1965).

Host plants. The sexual generation galls on *Quercus dentata* and *Q. serrata* (Monzen 1953, Kovalev 1965); the asexual generation galls on *Quercus serrata* (Katsuda & Yukawa 2003, Abe *et al*. 2007).

Gall location and structure. The sexual generation induces integral leaf galls, which produce from both sides of the leaf, 2.0–2.5 mm in diameter (Monzen 1953); the asexual generation induces bud galls (Katsuda & Yukawa 2003).

Phenology. The sexual adults emerge in May (Monzen 1953).

***Andricus mukaigawae* (Mukaigawa, 1913)**

Synonyms: *Dryophanta mukaigawae* Mukaigawa, 1913; *Andricus japonicus* Ashmead, 1904 (in Monzen 1931); *Andricus mukaigawae*: comb. nova in Abe (1986).

Lifecycle. Alternating asexual and sexual generations are known (Abe 1986).

Geographical distribution. Japan and China (Abe 1986, 2007, Pujade-Villar *et al.* 2016), Russia (Far East) (Kovalev 1965), probably North Korea (Kovalev 1965), South Korea (authors), India (West Kameng District) (Abe *et al*. 2012).

Host plants. *Quercus aliena*, *Q. dentata*, *Q. griffithii* Hook. F & Thomson ex Miq., *Q. mongolica* var. *grasseserrata* Rehid. et Wils., *Q. serrata* (Abe 1986, 2007, Wachi *et al*. 2012).

Gall location and structure. A single, bud urn-shaped gall, surrounded by numerous lanceolate spines, developed from axillary bud; maximum diameter 25 mm; single larval cell oval, embedded in an acorn-like cup, 3.5–4.0 mm in diameter and 6.0 mm high (Fig. A116). The sexual gall is a leaf gall, single ovoid, with a thin wall, produced on edge or midrib of leaf, inhibiting of development of surrounding leaf tissue; maximum diameter 2–3 mm (Abe 1986).

Phenology. The sexual generation galls appear on axillary buds in early June; mature in August; adults emerge in early December to early February. The sexual generation galls appear on the edges and midribs of leaves in early April, when leaf buds begin to break; adults emerge in late April. In late April and early May, females deposit their eggs in or on leaf primordia of immature axillary buds (Abe 1986). This species was studied in detail by Abe (1986, 1988, 1991, 1998, 2007, Wachi *et al*. (2012).

Similar galls. Galls resemble those of *Andricus targionii* which, however, are usually smaller in size (Abe 1986).

Andricus pseudocurvator Tang & Melika, 2011

Lifecycle. Only the sexual generation is known (Tang *et al*. 2011b).

Geographic distribution. Taiwan (Nantou and Taichung Counties). It is possible that this species also occur in continental China and Japan, where *Q. serrata* occurs (Tang *et al*. 2011b).

Host plants. *Quercus serrata* (Tang *et al*. 2011b).

Gall location and structure. Integral leaf galls. Individual galls approximately spherical, 2.4–3.6 mm in height, and integral to leaf lamina. Galls appear as yellowish or brownish dots on leaves, cause swelling on both upper and lower surfaces of leaf, each contains single thin-walled larval chamber, 1.6–2.3 mm in diameter. Outer wall of larval chamber attached to inner wall of surrounding gall tissue in both growing and mature galls. Galls usually occur separately on leaf and do not aggregate together (Figs A131–132). Young galls are fleshy, yellowish to brownish, remaining soft as they mature (Tang *et al*. 2011b)

Phenology. Galls mature in early March; adults emerge in mid and late March (Tang *et al*. 2011b).

Similar galls. The shape, structure and location of the gall is very similar to that induced by a Western Palearctic species, *Andricus curvator* Hartig, thus the species was named as "curvator-like" – *pseudocurvator* (Tang *et al*. 2011b).

Andricus pseudoflos (Monzen, 1954)

Synonyms: *Cynips pseudoflos* Monzen, 1954; *Adleria pseudoflos* (Monzen, 1954) (comb. nova in Kovalev (1965)). Judging from the life cycle, Abe (1986) considered that this species is synonymous with *A. targionii*. Later, Abe (2007) regarded this species as a distinct species based on cytological data and host plant exploitation, and transferred it into the genus *Andricus* (Monzen 1954).

Lifecycle. Only the asexual generation is known (Monzen 1954). The biology of this species was studied in detail by Abe (1986), Weih (1965), Wachi *et al*. (2012).

Geographic distribution. Japan, Korea, China and Russian Far East (Primorie) (Monzen 1954, Kovalev 1965, Weih 1965, Abe 1986, 2007, Abe *et al*. 2007).

Host plants. *Quercus dentata* (Monzen 1954, Kovalev 1965).

Gall location and structure. The gall is a flower-like deformation on the top of the twig or sometimes the midrib of the leaf (Fig. A133). The leaflet length is 40–60 mm, width 15 mm. The larval chamber oblong, length 6.0 mm, width 3.0 mm, side wall thin, smooth, yellowish (Monzen 1954).

Phenology. Galls begin to produce late in May, green and turn to yellowish brown in October; adults over-winter in galls and emerge in April or May next year (Monzen 1954).

Andricus quercicola Shinji, 1940

Lifecycle. Only the sexual generation is known (females were described only) (Monzen 1953).

Geographic distribution. Japan (Monzen 1953).

Host plants. *Quercus dentata* and *Q. serrata* (Monzen 1953).
Gall location and structure. The leaf swelling gall is rounded, yellowish, 3 mm in diameter. It is on the underside of the leaf, integral, unilocular. The larval chamber is in the tissue of the leaf blade (Monzen 1953).
Phenology. Adults emerge in late June of the same year when the gall was formed (Monzen 1953).

Andricus songshui Tang & Melika, 2011

Lifecycle. Only the sexual generation is known (Tang *et al*. 2011b).
Geographic distribution. Taiwan (Nantou County). It is possible that this species is also distributed in continental China and Japan where *Q. serrata* occurs (Tang *et al*. 2011b).
Host plants. *Quercus serrata* (Tang *et al*. 2011b).
Gall location and structure. Integral leaf galls, usually at the base of a leaf midrib. The swelling, on both unfolded young leaves and base of midrib, is 1.8–2.5 mm long (Fig. A134). Galls are usually yellowish and single; galls on unopened young leaves are green and in clusters of 1–3, multilocular (Figs A135–136). The two gall morphotypes can be found in the same month (Tang *et al*. 2011b).
Phenology. Galls mature in early March; adults emerge in mid to late March (Tang *et al*. 2011b).

Andricus targionii Kieffer, 1903

Synonyms: *Cynips pseudoflos* Monzen, 1954 (erroneously synonymised by Abe (1986)); *Adleria sakagamii* Kovalev, 1965 (synonymised by Abe (1986)).
Lifecycle. Only the asexual generation is known (Abe 1986, 2007, Weih 1965).
Geographical distribution. Japan, South Korea, China, Far East Russia (Kieffer 1903, Dalla Torre & Kieffer 1910, Kovalev 1965, Abe 1986, Abe *et al*. 2007)
Host plants. *Quercus aliena*, *Q. wutaishanica* Mayr (= *Q. liaotungensis* Koidz.) (Abe 1986, 2007, Abe *et al*. 2007).
Gall location and structure. The asexual bur shaped galls are on midribs, leaf margins, petioles and elongating shoots, usually clustered (Abe 2007).
Phenology. Galls mature in late summer; adults usually emerge from late October to late November (Abe 1986).
Similar galls. *Andricus mukaigawae* galls are similar, however, always bigger than galls of *A. targionii* (Abe 1986).

Andricus xishuangbannaus Melika & Tang, 2012

Lifecycle. Only the sexual generation is known (Tang *et al*. 2012b).
Geographic distribution. China (Xishuangbanna, Yunnan and Zhejiang Province) (Tang *et al*. 2012b, Wang *et al*. 2013a).
Host plants. *Quercus griffithii* (Tang *et al*. 2012b), *Q. serrata* (Wang *et al*. 2013a).
Gall location and structure. Integral blister leaf galls, always singular, never in clusters. The mature gall contains outer gall tissues and an inner, hollow-like larval chamber. The gall is approximately spherical, 2.4–3.6 mm in height, and the outer gall tissues protrude equally on both sides of leaf lamina (Figs A137–138). Outer wall of larval chamber attaches to the inner wall of surrounding gall tissues. Young gall is fleshy, yellowish to brownish, turning dry and dark brown when mature (Tang *et al*. 2012b).

Phenology. Galls mature in mid-April; adults emerge approximately one week later (Tang *et al*. 2012b).

Similar galls. Most closely resembles galls of *A. pseudocurvator,* however, galls of *A. xishuangbannaus* hollow-like, without separated larval chambers inside, whereas the galls of *A. pseudocurvator* are with free-rolling larval chambers inside (Tang *et al*. 2012b).

Belizinella Kovalev, 1965

Belizinella gibbera Kovalev, 1965

Synonyms. *Belizinella gibbera* Kovalev, 1965. *Trigonaspis gibbera*: Melika & Abrahamson (2002); *Belizinella gibbera* Kovalev, 1965, comb rev. in Melika (2012).

Lifecycle. Only the asexual generation is known. Females are wingless (Kovalev 1965, Melika 2012).

Geographic distribution. Russian Far East (Kovalev 1965).

Host plants. *Quercus dentata* (Kovalev 1965).

Gall location and structure. Detachable spherical leaf galls on the underside of the leaves, with glabrous surface, 10–12 mm in diameter, unilocular (Fig. A139), with a larval chamber in the center of the gall, 2.5 mm in diameter (Kovalev 1965).

Phenology. Adults emerge in November (Kovalev 1965).

Belizinella vicina Kovalev, 1965

Synonyms. *Belizinella vicina* Kovalev, 1965. *Trigonaspis vicina*: Melika & Abrahamson (2002); *Belizinella vicina* Kovalev, 1965, comb rev. in Melika (2012).

Lifecycle. Only the asexual generation is known; females are wingless (Kovalev 1965, Melika 2012).

Geographic distribution. Russian Far East (Kovalev 1965).

Host plants. *Quercus mongolica* (Kovalev 1965).

Gall location and structure. Leaf galls, very similar to those induced by *B. gibbera*, but are smaller when mature (Kovalev 1965).

Phenology. Galls mature in August; adults emerge in February of the following year (Kovalev 1965).

Biorhiza Westwood, 1840

Biorhiza nawai (Ashmead, 1904)

Synonyms: *Biorhiza weldi* Yasumatsu & Matsuda, 1955 (in Pujade-Villar *et al*. 2003).

Lifecycle. Only the sexual generation is known (Monzen 1954).

Geographic distribution. Japan (Ashmead 1904, Monzen 1954), South Korea (Abe *et al*. 2007); Russia (Far East) (Kovalev 1965), China (Beijing Province) (Abe *et al*. 2007).

Host plants. *Quercus mongolica, Q. serrata* (Monzen 1954, Kovalev 1965).

Gall location and structure. Bud gall on the top of a twig The gall is large, globose, about 2 cm in diameter, succulent, polythalamus, inseparable, green in colour, with reddish tinge on sunny side, turns yellowish in summer (Fig. A140) (Monzen 1954).

Phenology. Adults emerge in June-July (Monzen 1954, Kovalev 1965).

Callirhytis Förster, 1869

Callirhytis glanduliferae Monzen, 1953

Lifecycle. Only females are known (Monzen 1953).
Geographic distribution. Japan (Monzen 1953).
Host plants. *Quercus serrata* (Monzen 1953).
Gall location and structure. The gall is hemispherical, on the underside of leaves, the free surface convex, attached part flat, diameter about 4 mm, yellowish when fresh, turns to yellowish or reddish brown when mature, smooth, hard, monothalamus, the larval chamber in the center of the gall (Fig. A141) (Monzen 1953**).**
Phenology. Galls mature in October; adults emerge next year in May (Monzen 1953)**.**

Cerroneuroterus Melika & Pujade-Villar, 2010

Cerroneuroterus folimargo (Monzen, 1954)

Synonyms. *Neuroterus folimargo* Monzen, 1954. *Cerroneuroterus folimargo*: Melika *et al.* (2010).
Lifecycle. Alternating sexual and asexual generations are known. The asexual generation was described by Monzen (1954); the sexual generation was experimentally obtained by Yukawa & Masuda (1996).
Geographic distribution. Japan and Taiwan (Melika *et al*. 2010).
Host plants. *Quercus acutissima* Carruth., *Q. variabilis* Blume (Melika *et al*. 2010).
Gall location and structure. The asexual spangle gall is located on the end of a vein or spine of the leaf, on the underside, pale pinkish, conical, 2 mm in diameter (Fig. A142). Sexual generation galls are tiny catkin galls (Yukawa & Masuda 1996).
Phenology. Asexual females emerge in April and induce tiny catkin galls; sexual generation adults emerge in late May (Melika *et al.* 2010).
Similar galls. The asexual spangle gall very similar to the gall of *C. vonkuenburgi* (Dettmer), but in *C. folimargo*, the gall is located always at the leaf edge, at the end of veins with only a single gall per leaf (Fig. A142) (Melika *et al.* 2010). The sexual generation galls are very similar to those of *C. monzeni* (Dettmer) (Melika *et al.* 2010).

Cerroneuroterus monzeni (Dettmer, 1934)

Synonyms: *Neuroterus monzeni* Dettmer, 1934. *Cerroneuroterus monzeni*: Melika *et al.* (2010).
Lifecycle. Alternating sexual and asexual generations are known. The sexual females were originally described by Dettmer (1934). Later, Monzen redescribed the sexual generation including males (Monzen 1954). Yukawa & Masuda (1996) experimentally matched the sexual and the asexual generations.
Geographic distribution. Japan (Dettmer 1934, Monzen 1954).
Host plants. *Quercus acutissima* and *Q. variabilis* (Dettmer 1934, Monzen 1954).
Gall location and structure. Sexual generation galls on catkins; small, conical, yellowish, smooth, with few setae, thin walled, unilocular, 2 mm in diameter. Small asexual spangle galls develop on the underside of leaves (Fig. A67).
Phenology. The asexual females overwinter in the galls, adults emerge in March-April and induce catkin galls from which the adults emerge in May of the same year (Monzen 1954, Melika *et al*. 2010).

Similar galls. Similar in shape to those induced by the Western Palearctic species *N. numismalis*, rounded and flattened with a central dimple, dark red point, without fringe of hair around the gall. Also similar to *C. folimargo*.

***Cerroneuroterus vonkuenburgi* (Dettmer, 1934),**

Synonyms. *Neuroterus vonkuenburgi* var. *wakayamensis* Monzen (in Abe *et al*. (2007)). *Cerroneuroterus vonkuenburgi*: Melika *et al*. (2010); *Andricus asakawae* Sninji, 1943 (in Yukawa & Masuda 1996); *Andricus kanagawae* Shinji, 1943 (in Yukawa & Masuda 1996); *Neuroterus bonihenrici* Dettmer, 1934 (in Yukawa & Masuda 1996); *Neuroterus* (=*Neoneuroterus*) *kashiyamai* (Monzen, 1954) (in Yukawa & Masuda 1996); *Dryophanta mitsukurui* Ashmead, 1904 (in Yukawa & Masuda 1996).

Lifecycle. Alternating sexual and asexual generations are known. The sexual generation was experimentally obtained by Yukawa & Masuda (1996).

Geographic distribution. Japan (Ashmead 1904, Dettmer 1934, Monzen 1954, Yukawa & Masuda 1996) and Taiwan (Melika *et al*. 2010).

Host plants. *Quercus acutissima* and *Q. variabilis* (Melika *et al*. 2010).

Gall location and structure. The asexual galls are on the underside of leaves, yellowish or reddish brown, subspherical, thinner toward the apex and somewhat dilated at the top, densely pubescent, diameter 4–6mm, gall wall thick, monothalamus, larval chamber 1.5 mm in diameter, separable (Monzen 1954; Fig. A66). Sexual galls form large woolly masses on catkins (Melika *et al*. 2010). The flower gall, a sponge like ball, diameter 15–25 mm (Fig. A143). Each larval chamber small, oblong, yellowish, thin-walled, covering with woolly hairs, forming a bunch at an edge especially. The chamber 3x2 mm, the hairs 5–6 mm (Monzen 1954).

Phenology. The sexual wasps emerge in late May to early June (Monzen 1954). Asexual spangle galls mature in early November; adults emerge from late November; females were observed to lay eggs from late January (Melika *et al*. 2010).

Cyclocynips Melika, Tang, &Sinclair, 2013

Cyclocynips uberis Melika &Tang, 2013

Lifecycle. Only the asexual generation is known (Melika *et al.* 2013).

Geographic distribution. Taiwan (Fuhsing Township, Taoyuan County) (Melika *et al*. 2013).

Host plants. *Quercus longinux* Hayata (*Quercus* subgenus *Cyclobalanopsis*) which is endemic to Taiwan, thus raising the possibility that *Cyclocynips uberis* may also be endemic (Melika *et al*. 2013).

Gall location and structure. Multi-chambered twig swellings up to 10–15 cm long and twice the diameter of unaffected parts of the twig (Fig. A144). Larval chambers are 1.3–2.0 mm long and 0.2–0.5 mm in diameter, located under the bark at various depths throughout the twig. The orientation of the longitudinal axis of the larval chamber varies but is usually parallel to the shoot axis (Fig. A145). The bark of the affected shoot is unaffected, and other than the larval chambers there are no obviously differentiated complex gall tissues within the shoot (Melika *et al.* 2013).

Phenology. Adults emerge in March (Melika *et al.* 2013).

Similar galls. These galls broadly resemble those induced by the asexual generation of *Plagiotrochus masudai* and *P. glaucus* (Melika *et al.* 2013).

Cyclocynips tumorvirgae Melika &Tang, 2013

Lifecycle. Only the asexual generation is known (Melika *et al.* 2013).
Geographic distribution. Taiwan (Shihding District, New Taipei City) (Melika *et al*. 2013).
Host plants. *Quercus glauca* Thunb. in Murray (*Quercus* subgenus *Cyclobalanopsis*) (Melika *et al*. 2013).
Gall location and structure. Galls develop as multichambered swellings within twigs. Larval chambers are 2.1–2.6 mm long and 1.2–1.6 mm in diameter, always appear to be close to the twig surface and orientated along its axis, unlike those of *C. uberis* that can occur at varying depths and orientations (Fig. A146) (Melika *et al*. 2013).
Phenology. Adults emerge in March (Melika *et al*. 2013).
Similar galls. Galls are similar to those induced by *C. uberis*.

Cycloneuroterus Melika & Tang, 2011

Cycloneuroterus abei Melika &Tang, 2016

Lifecycle. Only the sexual generation is known (Tang *et al*. 2016a).
Geographic distribution. Taiwan (Shihding District, New Taipei City; Taoyuan County; Heping District, Taichung City) (Tang *et al.* 2016a).
Host plants. *Quercus glauca* and *Q. globosa* (Tang *et al*. 2016a).
Gall location and structure. The gall is an integrated young leaf swelling, protruding on both sides of the leaf blade (on *Q. glauca* galls were found to grow on the leaf petiole). The gall is 2.5–6.0 mm in diameter, with a single or multiple larval chambers. Sometimes the gall growth causes distortion of leaves (Figs A147–148) (Tang *et al.* 2016a).
Phenology. Gall growth coincides with the point of host sprouting in mid-February. Galls develop to largest size when the host leaves wholly expanded; adults emerge in late March till mid-April (Tang *et al.* 2016a).

Cycloneuroterus akagashiphilus Ide, Wachi & Abe, 2012

Lifecycle. Only the sexual generation is known (Ide *et al.* 2012).
Geographic distribution. Japan (Kyushu) (Ide *et al*. 2012).
Host plants. *Quercus acuta* Thunb. (*Quercus* subgenus *Cyclobalanopsis*) **(**Ide *et al.* 2012).
Gall location and structure. Galls on lateral margin or apex of young leaf just after bud burst in late May. Oval gall 2.0 mm in diameter, , usually two to eight galls clustered. Immature galls yellowish green, mature ones are brown **(**Ide *et al.* 2012).
Phenology. Gall mature in late March-April; adults emerge from late May to early June **(**Ide *et al.* 2012).

Cycloneuroterus arakashiphagus Ide,Wachi & Abe, 2012

Lifecycle. Alternating sexual and asexual generations are known (Yukawa & Masuda 1996, Ide *et al*. 2012).
Geographic distribution. Japan (Honshu, Shikoku, Kyushu) (Yukawa & Masuda 1996, Ide *et al.* 2012).
Host plants. *Quercus glauca* (Ide *et al*. 2012).
Gall location and structure. The sexual generation galls develop in sprouts, while the galls of the asexual generation – on leaf veins. The sexual generation galls are oval, pale green, or

yellowish brown, 1.5–2.0 mm in diameter and 2.0–2.5 mm in height, usually clustered (Ide *et al.* 2012).

Phenology. The adult of the asexual generation is unknown. Galls of the sexual generation appear in early April; adults of the sexual generation emerge in mid-April. The gall of the asexual generation begins to appear on the leaf veins in early June; after maturation, the asexual generation gall falls to the ground **(**Ide *et al*. 2012).

Cycloneuroterus ergei **Tang & Melika, 2016**

Lifecycle. Only the sexual generation is known (Tang *et al.* 2016a).

Geographic distribution. Taiwan (Mt. Erge, Shihding District, New Taipei City) (Tang *et al.* 2016a).

Host plants. *Quercus salicina* Blume (*Quercus* subgenus *Cyclobalanopsis*) (Tang *et al*. 2016a).

Gall location and structure. Galls are on young sprouts, unilocular, pinkish or yellowish, 2.0–2.5 mm in length (Figs A149) (Tang *et al*. 2016a).

Phenology. Galls mature in late March; adults emerge from galls immediately after field collection (Tang *et al*. 2016a).

Cycloneuroterus formosanus **Tang & Melika, 2011**

Lifecycle. Only the sexual generation is known (Tang *et al*. 2011a).

Geographic distribution. Taiwan (Taichung, Nantou, and Taitung Counties).

Host plants. *Lithocarpus konishii* (Hayata) Hayata (Tang *et al*. 2011a).

Gall location and structure. The gall is an irregular stem-swelling that only appears on young spring growth. The gall causes a swelling, occuring both along shoots or in terminal buds, and young leaves remain on both swollen shoots or swollen terminal buds (Figs A150–151). Each gall is multilocular and coloured red with a slight purple tinge. The gall can grow to a length of 25 mm. The young gall is fleshy and juicy, remaining soft until adults emerge (Tang *et al*. 2011a).

Phenology. Mature galls were collected from early to mid April; adults emerge immediately after gall collection under laboratory conditions (Tang *et al.* 2011a).

Comments. Formally only the sexual generation is known (Tang *et al*. 2011a). However, sequences of cytb and ITS2 genes showed that this species has an alternate asexual generation which is developing also on *L. konishii* and produces detachable leaf galls (Fig. A152). No adult wasps were obtained yet from these galls and thus the asexual generation formally is not described yet.

Cycloneuroterus fortuitusus **Tang & Melika, 2011**

Lifecycle. Only the sexual generation is known (Tang *et al*. 2011a).

Geographic distribution. Taiwan (Taitung County) (Tang *et al*. 2011a) and Japan (Kitayama, Kofu City, Yamanashi Prefecture and Mt. Sakurei, Saga Prefecture) (Ide *et al.* 2012). It is possible that this species is also distributed on the Asian continent where *Q. glauca* occurs (Himalaya to Japan and Vietnam (Govaerts & Frodin 1998)).

Host plants. *Quercus glauca* (Tang *et al*. 2011a).

Gall location and structure. Integral swelling-like galls in the leaf petiole (Fig. A153). The gall is cryptic, occuring at the base of a newly grown shoot that is still covered by many bud scales. The gall causes a slight swelling at the base of the young shoot; unless the bud scales are removed, it is difficult to detect the presence of the gall (Tang *et al*. 2011). The gall is 3 mm in

height and 1.5mm in diameter. Sometimes two galls occur together at the base of the same young shoot (Tang *et al*. 2011a).
Phenology. Galls mature in late February; adults emerge in early March (Tang *et al*. 2011a).

Cycloneuroterus gilvus **Melika & Tang, 2016**
Lifecycle. Only the sexual generation is known (Tang *et al*. 2016a).
Geographic distribution. Taiwan (Hsinchu and Taoyuan Counties) (Tang *et al*. 2016a).
Host plants. *Quercus gilva* Blume (*Quercus* subgenus *Cyclobalanopsis*) (Tang *et al.* 2016a).
Gall location and structure. The gall is hollow or blister-like on folded or unfolded young leaves. Galls with a single larval chamber, usually numerous galls develop on one leaf, pinkish or rusty in color (Figs A154–155). Galls are 3.0–4.7 mm in diameter and 2.2–4.8 mm in height (Tang *et al*. 2016a).
Phenology. The gall development coincides with host sprouting in mid-March ; adults emerge from late March to early April (Tang *et al.* 2016a).

Cycloneuroterus globosus **Melika & Tang, 2016**
Lifecycle. Only the sexual generation is known (Tang *et al*. 2016a).
Geographic distribution. Taiwan (Nantou County). The host-plant, *Q. globosa* is endemic to Taiwan, thus *C. globosus* might be also endemic to Taiwan (Tang *et al*. 2016a).
Host plants. *Quercus globosa* (Tang *et al*. 2016a).
Gall location and strucrure. Galls are red pimples on midribs or lateral veins of young leaves. In some cases the gall development disrupts the sprouting and galls are forming a tuft on a bud (Figs A156–158). Galls are unilocular, 1.0–1.7 mm in width and 1.6–3.3 mm in length (Tang *et al.* 2016a).
Phenology. The gall development coincides with sprouting from mid- to late-March; adults emerge under laboratory conditions immediately after the galls were collected in the field (Tang *et al*. 2016a).

Cycloneuroterus hisashii **Ide, Wachi & Abe, 2012**
Lifecycle. Only the sexual generation is known **(**Ide *et al*. 2012).
Geographic distribution. Japan (Honshu) (Yukawa & Masuda 1996, Ide *et al*. 2012).
Host plants. *Quercus glauca* (Ide *et al.* 2012).
Gall location and structure. The gall is in the basal portion of a bud, globular, 5–7 mm in diameter and 10–13 mm in height. Galled bud somewhat swollen, with 15 or less larval chambers **(**Ide *et al.* 2012).
Phenology. Galls mature from mid- to late April; adults emerge in early May **(**Ide *et al.* 2012).

Cycloneuroterus jianwui **Tang & Melika, 2016**
Lifecycle. Only the sexual generation is known (Tang *et al*. 2016a).
Geographic distribution. China (Yunnan Province, Lan Cang Co., Mt. Xinghou) (Tang *et al*. 2016a).
Host plants. The host plant species is unknown but it was definitely a species from *Quercus* subgenus *Cyclobalanopsis* (Tang *et al*. 2016a).
Gall location and structure. The gall growth causes young leaves highly distorted; those leaves usually occur on the tip of the twigs (Fig. A159). Galls are multilocular, 2.0–2.5 mm in diameter and 1.5–2.0 mm in height (Tang *et al*. 2016a).

Phenology. Galls appear in the period of active sprouting; adults emerge in April (Tang *et al*. 2016a).

***Cycloneuroterus lilungi* Tang, Melika & Yang, 2011**

Lifecycle. Only the sexual generation is known (Tang *et al.* 2011a).

Geographic distribution. Taiwan (Pingtung and Hsinchu Counties). The host plant, *Q. longinux*, is known only from Taiwan (Govaerts & Frodin 1998), so it is possible that this species is endemic to Taiwan (Tang *et al*. 2011).

Host plants. *Quercus longinux* (Tang *et al.* 2011a).

Gall location and structure. Integral leaf galls. The young galls are red, succulent pimples on young leaves with central larval chamber. Mature galls are brownish and hollow, without conspicuous central larval chamber (Figs A160). Diameter of galls is 0.8–1.6 mm. The tissues surrounding larval chamber are swollen and cause deformation of leaves (Tang *et al.* 2011a).

Phenology. Galls mature in early and mid-February; adults emerge from late February till early March (Tang *et al*. 2011a).

***Cycloneuroterus lirongchiuea* Melika & Tang, 2011**

Lifecycle. Only the sexual generation is known (Tang *et al*. 2011a).

Geographic distribution. Taiwan (Taitung County). *Quercus hypophaea* Hayata is known only from Taiwan (Govaerts & Frodin 1998), so it is possible that this species is endemic to Taiwan (Tang *et al.* 2011a).

Host oaks: *Q. hypophaea* (*Quercus* subgenus *Cyclobalanopsis*) (Tang *et al*. 2011a).

Gall location and structure. Galls are integral to leaf blades of young leaves with swelling on both sides of the leaf. They are brownish, 3–4 mm in diameter and extending up to 2.7 mm from the leaf surface. Galls grow individually on a leaf rather than aggregated together (Figs A161–162). Gall tissue is succulent when young and the gall becomes hollow once the larva matures and pupates inside. The pupa can roll freely inside the gall (Tang *et al*. 2011a).

Phenology. Galls mature from early March until early April; adults emerge under laboratory conditions over the same time period (Tang *et al*. 2011a).

***Cycloneuroterus lohsei* Melika & Tang, 2016**

Lifecycle. Alternating sexual and asexual generations are known (Tang *et al.* 2016a).

Geographic distribution. Taiwan (Shihding District, New Taipei City; Hsinchu County) (Tang *et al.* 2016a).

Host plants. *Quercus sessilifolia* Blume (*Quercus* subgenus *Cyclobalanopsis*) for the sexual generation and *Q. gilva* (*Quercus* subgenus *Cyclobalanopsis*) for the asexual generation galls (Tang *et al.* 2016a).

Gall location and structure. Galls of the sexual generation are multilocular, fully covered with pink or white hairs, and on young leaves. The gall growth sometimes causes the deformation of the whole leaf. The swollen parts on leaves are 10.0–20.0 mm long and 4.0–6.0 mm broad (Figs A163–164). Asexual generation galls are multilocular, rounded clusters on the midrib on the lower surface of mature leaves and densely covered in brown hairs, 4–5 mm long (Fig. A165) (Tang *et al.* 2016a).

Phenology. Sexual generation galls appear on the host-plant in March; adults emerge from late-March to mid-April. Asexual generation galls have not been reared successfully, so asexual adults are unknown. However, DNA sequences obtained from larvae dissected from asexual galls match those from sexual generation adults. Asexual generation galls have been collected in August (Tang *et al.* 2016a).

***Cycloneuroterus longinuxus* Tang & Melika, 2011**
Lifecycle. Only the sexual generation is known (Tang *et al*. 2011a).
Geographic distribution. Taiwan (New Taipei City, Hsinchu, Nantou, and Taitung Counties).
Host plants. *Quercus longinux* (Tang *et al*. 2011a).
Gall location and structure. Integral leaf galls. The gall is a multilocular cluster of many small spherical swellings extending to both sides of the leaf blade. The gall tissue is succulent and soft until the adults emerge and coloured the same as the leaf (Fig. A166). Viewed from the upper side, the swollen section of leaf is 6–10 mm in width and 12mm long. After the emergence of adults the gall turns liginified and brownish (Tang *et al*. 2011a).
Phenology. Galls mature in early March; adults emerge under laboratory conditions immediately after collecting (Tang *et al*. 2011a).

***Cycloneuroterus tumiclavus* Tang & Melika, 2016**
Lifecycle. Only the sexual generation of this species is known (Tang *et al.* 2016a).
Geographic distribution. Taiwan (Heping District) (Tang *et al.* 2016a).
Host plants. *Quercus glauca* (Tang *et al*. 2016a).
Gall location and structure. The galls are on the adaxial end of the catkin spike, yellow green, oval-shaped swellings densely covered with hairs, 3.0–3.5 mm in length and 1.5–2.0 in width (Fig. A167). Galls are unilocular (Tang *et al.* 2016a).
Phenology. Galls mature in late March; adults emerge under laboratory conditions immediately after the galls were transferred to the laboratory for rearing (Tang *et al.* 2016a).

***Cycloneuroterus uraianus* Tang & Melika, 2016**
Lifecycle. Only the sexual generation is known (Tang *et al*. 2016).
Geographic distribution. Taiwan (Taoyuan County, Fushing Township) (Tang *et al*. 2016a).
Host plants. *Castanopsis uraiana* (Hayata) Kaneh. & Hatus (Tang *et al.* 2016a).
Gall location and structure. Bud galls. Galls are cryptic and embedded in buds with 2–15 cells clustered together. Infected buds remain their intact appearance and it is difficult to detect whether the bud was infected or not (Fig. A168) (Tang *et al.* 2016a).
Phenology. Galls mature in late March; adults emerge from late March till early April (Tang *et al*. 2016a).

***Cycloneuroterus wangi* Abe, Ide, & Odagiri, 2014**
Lifecycle. Only the asexual generation is known (Abe *et al*. 2014a).
Geographic distribution. Southeastern China (Nanling National Forest Park, Ruyuan, Shaoguan, Guangdong) (Abe *et al.* 2014a).
Host plants. *Q. sessilifolia* (Abe *et al.* 2014a).
Gall location and structure. Galls unknown.
Phenology. Adults were collected in December (Abe *et al*. 2014a).

Cynips Linnaeus, 1758

***Cynips staminobia* Kovalev, 1965**
Lifecycle. Only the sexual generation is known (Kovalev 1965).

Geographic distribution. Far East Russia (Kovalev 1965).
Host plants. *Quercus mongolica* (Kovalev 1965).
Gall location and structure. Rounded unilocular catkin galls with white hairs, 3 mm in diameter (Kovalev 1965).
Phenology. Adults emerge in early June (Kovalev 1965).

Dryocosmus Giraud, 1859

Dryocosmus carlesiae Tang & Melika, 2011

Lifecycle. Only the sexual generation is known (Melika *et al*. 2011).
Geographic distribution. Taiwan (Taitung and Pingtung Counties) (Melika *et al*. 2011).
Host plants. *Castanopsis carlesii* (Hemsley) Hayata (Melika *et al*. 2011).
Gall location and structure. Unilocular galls develop from leaf buds or on leaves. The body of the gall located on a long, thin stalk, 10–20 mm long, growing out from the bud or forming within the leaf petiole. The body of the gall rounded, spherical, 7.0–8.3 mm in diameter. The gall is green with the surface smooth, shiny, mottled with some whitish irregular spots (Figs A169–170). The parenchyma of the gall is green, juicy, with a centrally located larval chamber, 3.0–3.5 mm in length and diameter usually half of the length (Melika *et al.* 2011).
Phenology. Galls appear on the tree from early March, mature by mid- to late March; adults emerge in April (Melika *et al*. 2011).

Dryocosmus kunugiphagus Ide & Abe, 2015

Lifecycle. Alternate sexual and asexual generations are known (Ide & Abe 2015).
Geographic distribution. Japan (Honshu, Shikoku, Kyushu) and Korea (Yukawa & Masuda 1996, Ide & Abe 2015).
Host plants. *Quercus acutissima* (Ide & Abe 2015).
Gall location and structure. Asexual generation galls usually are clustered on twig, each gall is unilocular, spherical, 5–6 mm in diameter. Sexual generation unilocular spherical galls are on shoot apex.
Phenology. Sexual generation galls are induced when shoots of the host plant elongate and galls reach maturation in late May; adults emerge in early June. Adult females oviposit into the previous year's shoot. Asexual generation galls begin appearing in early August; adults emerge between late March and early April (Ide & Abe 2015).

Dryocosmus kuriphilus Yasumatsu, 1951

Lifecycle. Only the asexual generation is known (Murakami 1980).
Geographic distribution. *Dryocosmus kuriphilus* was formally described in 1951 (Yasumatsu 1951), but was first observed in China in 1929 (Murakami 1980). Murakami (1980) concluded that this gallwasp is indigenous to China and was accidentally introduced to Japan in *c*. 1941 (Yasumatsu 1951), Korea in 1958 (Tamura 1962, Cho & Lee 1963), the USA in 1974 (Payne *et al*. 1975, 1976), Europe (Piedmont, Italy) in 2002 (Brussino *et al.* 2002), Nepal (Ueno 2006) and Taiwan in 2010 (Tang 2015). The history of its introduction worldwide and particularly in Europe is described in depth by Aebi *et al*. (2006). Currently *D. kuriphilus* spreaded throughout Europe, where *Castanea* spp. is growing (Kos *et al*. 2015, Radócz *et al*. 2015).
Host plants. Originally in China *D. kuriphilus* trophically associated with *Castanea crenata* Siebold in Zucc., *C. henryi* (Skan), *C. mollissima* Blume, *C. seguinii* Dode. Later on, after

accidental introduction to the USA and Europe, the pest shifted also onto *C. dentata* (Marshall) Borkh. and *C. sativa* Mill. respectively (Brussino *et al*. 2002).

Gall location and structure. Subglobular, succulent, and fleshy integral multilocular galls on young buds and leaf petiole or leaf midrib. Galls are usually green, about 5.0 mm in width by 5.0–15.0 mm in length (Fig. A171). The average number of larval chambers per gall is 1.5–3.0 (Brussino *et al*. 2002).

Phenology. Asexual female *D. kuriphilus* emerges in early summer and lays eggs in buds of chestnut trees; the first-instar larvae are overwintering in the buds, and galls start to develop in spring at bud burst; adults emerge in June-August (Brussino *et al*. 2002).

***Dryocosmus nanlingensis* Abe, Ide, & Odagiri, 2014**

Lifecycle. Only the sexual generation is known (Abe *et al.* 2014a).

Geographic distribution. Southeastern China (Nanling National Forest Park, Ruyuan, Shaoguan, Guangdong) (Abe *et al*. 2014a).

Host plants. Unknown.

Gall location and structure. Unknown.

Phenology. Adults emerge in December (Abe *et al*. 2014a).

***Dryocosmus okajimai* Abe, Ide, Konishi & Ueno, 2014**

Lifecycle. Only the sexual generation is known (Abe *et al*. 2014b).

Geographic distribution. Vietnam (Tuyen Lam Lake, Da Lat, Lam Dong Province) (Abe *et al.* 2014b).

Host plants. Unknown.

Gall location and structure. Unknown.

Phenology. Adults emerge in July (Abe *et al.* 2014b).

***Dryocosmus pentagonalis* Melika & Tang, 2011**

Lifecycle. Only the sexual generation is known (Melika *et al*. 2011).

Geographic distribution. Taiwan (Taitung County) (Melika *et al*. 2011).

Host plants. *Castanopsis carlesii* (Melika *et al.* 2011).

Gall location and structure. Galls are forming on buds, catkins and young leaves. On catkins this gall causes thickening of the petiole, with the base of the gall inserted in a shallow depression. An elongated, spindle-shaped unilocular gall reaching a length of 8–10 mm and a diameter of 2–4 mm when mature. The gall is attached by a stalk of variable length (commonly 4–12 mm) (Figs A172–173). The main body of the gall is marked with longitudinal ribs, usually five, and thus from the top view the gall is star-shaped (Melika *et al.* 2011).

Phenology. Galls appear on the tree from early March, mature by mid-March; adults emerge in late March to the first week of April (Melika *et al.* 2011).

Similar galls. The gall closely resembles the asexual galls of three Western Palearctic *Andricus* species: *A. callidoma* (Hartig), *A. malpighii* (Adler) and *A. seminationis* (Giraud); structurally the last one is the most similar (Melika *et al.* 2011).

***Dryocosmus sakureiensis* Ide, Wachi & Abe, 2013**

Lifecycle. Only the sexual generation is known (Ide *et al*. 2013).

Geographic distribution. Japan (Kyushu) (Ide *et al*. 2013).

Host plants. *Quercus* sp. (*Quercus* subgenus *Cyclobalanopsis*) (Ide *et al*. 2013).

Gall location and structure. One to three galls in one bud. Oval, 2.5–4.0 mm in height, 1.5–2.0 mm in diameter. Young galls yellowish green, mature ones brown. Apex of galled bud sometimes more or less bent (Ide *et al*. 2013).
Phenology. Galls mature from late April to early May; adults emerge from mid- to late May (Ide *et al*. 2013).

***Dryocosmus sefuriensis* Ide, Wachi & Abe, 2013**
Lifecycle. Only the sexual generation is known (Ide *et al*. 2013).
Geographic distribution. Japan (Kyushu) (Ide *et al.* 2013).
Host plants. *Quercus acuta* Thunb. (*Quercus* subgenus *Cyclobalanopsis*) (Ide *et al*. 2013).
Gall location and structure. One to three galls on one young sprout. Gall irregularly swollen, pubescent; sprout with gall shortened and swollen. Young galls yellowish green and turn brown when mature; one gall contains 3-6 larval chambers, each larval chamber 1.5–2.0 mm in diameter (Ide *et al.* 2013).
Phenology. Galls mature in late May; adults emerge in late May to early June (Ide *et al.* 2013).

***Dryocosmus squamus* (Monzen, 1953), comb. nova**
Synonyms. *Andricus squama* Monzen, 1953. *Dryocosmus squamus* (Monzen, 1953), **comb. nova.**
Lifecycle. Only the sexual generation is known (Monzen 1953).
Geographic distribution. Japan (Iwate Prefecture) (Monzen 1953).
Host plants. *Quercus serrata* (Monzen 1953).
Gall location and structure. The bud gall is small, oblong, diameter about 4–6 mm, height 4.5 mm, the surface is covered with microscopical scales, yellowish brown; the gall wall rather thick, with 1–3 larval chambers (Monzen 1953, Yukawa & Masuda 1996).
Phenology. Adults emerge in late May (Monzen 1953).
Comments. Three females were found in the Monzen collection at the Kyoto University by G.Melika. They are all *Dryocosmus* and not *Andricus* (the mesoscutum is smooth, without surface sculpture, scuto-scutellar articulation present, the mesoscutellum without scutellar foveae, only a semilunar depression anteriorly present on the mesoscutellum).

***Dryocosmus testisimilis* Tang & Melika, 2011**
Lifecycle. Only the sexual generation is known from galls (Melika *et al*. 2011).
Geographic distribution. Taiwan (New Taipei City, Taoyuan and Hsinchu Counties) (Melika *et al*. 2011).
Host plants. *Castanopsis uraiana* (Melika *et al*. 2011).
Gall location and structure. Galls on leaves, 22–31 mm in length and 12–21 mm in diameter. The parenchyma of the gall is green, juicy, with many larval chambers gather centrally. Each larval chamber is 2.5– 3.0 mm in length and 1.7–2.0 mm in diameter. Multilocular. The length of the gall body usually encompasses around 2/3 of the entire length of the gall, including the length of the stalk (Fig. A174) (Melika *et al*. 2011).
Phenology. Galls mature in mid- and late-March; adults emerge in April-May (Melika *et al*. 2011).

***Dryocosmus triangularis* Melika & Tang, 2011**
Lifecycle. Only the sexual generation is known (Melika *et al.* 2011).

Geographic distribution. Taiwan (Taitung County) (Melika *et al.* 2011).
Host plants. *Castanopsis carlesii* (Melika *et al*. 2011).
Gall location and structure. Galls are forming on buds, catkins, and young leaves (Melika *et al*. 2011). The gall has only three distinct longitudinal ribs, thus has a triangular cross-section; 4.5–7.0 mm long, 1.2–1.9 mm width in crosssection; the stalk is usually much shorter than in *D. pentagonalis*, only 2–3mm long (Fig. A175) (Melika *et al*. 2011).
Phenology. Galls appear on the tree from early March, mature in mid-March; adults emerge in late March-April (Melika *et al*. 2011).

Dryocosmus zhuili **Liu & Zhu, 2015**
Lifecycle. Only the sexual generation is known (Zhu *et al*. 2015).
Geographic distribution. Southeastern China (Fujian province) (Zhu *et al*. 2015).
Host plants. *Castanea henryi* (Zhu *et al*. 2015).
Gall location and structure. Subglobular, succulent, and fleshy integral galls are formed on young buds and leaf petiole and midrib of leaves close to leaf base on new shoots. Galls are usually green, occasionally rosy on the sunny side; about 8.0 mm in width by 8.0–25.0 mm in length (Figs 4–6 in Zhu *et al*. 2015).
Phenology. The same as in *D. kuriphilus*.
Similar galls. It is impossible to distinguish galls and adults from *D. kuriphilus*.

Twelve *Dryocosmus* species from China and Taiwan were recently described (Tang *et al*. 2016c, accepted)

Latuspina Monzen, 1954

Latuspina abemakiphila **Ide & Abe, 2016**
Lifecycle. Only the sexual generation is known (Ide & Abe 2016).
Geographic distribution. Japan (Honshu, Shikoku) (Ide & Abe 2016, Yukawa & Masuda 1996).
Host plants. *Quercus variabilis* (Ide & Abe 2016).
Gall location and structure. Several to a dozen galls are clustered on leaf blade; pale green, blister-like, 1.5–2.5 mm in diameter, 1.5mm in height on upper side, white, circular disk-like, 4.0–5.0mm in diameter, 1.0–2.0 mm in height on lower side, containing one larval chamber (Ide & Abe 2016).
Phenology. Galls appear in mid-April; adults emerge from late April to early May (Ide & Abe 2016).

Latuspina acutissimae **Wang, Pujade-Villar & Guo, 2016**
Lifecycle. Only the sexual generation is known (Wang et al. 2016b).
Geographic distribution. Currently known from China: Zhejiang (Wang et al. 2016b).
Host plants. *Q. acutissima* (Wang et al. 2016).
Gall location and structure. Unilocular integrated pabrenchima leaf galls. The young growing gall is juicy, spherical, green with black spots, with small surface tubercles, compressed if closely clustered. The mature gall is brown, up to 1.2 mm in diameter with hard walls (Wang et al. 2016b).

Phenology. Galls are appearing on the tree from early May, maturing through the summer and in late October. Under the laboratory conditions, adults emerge from late September (Wang et al. 2016).

***Latuspina atamiensis* (Ashmead, 1904)**

Synonyms: *Neuroterus atamiensis* Ashmead, 1904; *Latuspina atamiensis*: Ide & Abe (2016).

Lifecycle. Alternating sexual and asexual generations are known (Ide & Abe 2016).

Geographic distribution. Japan (Honshu, Kyushu) (Ide & Abe 2016).

Host plants. *Quercus acutissima, Q. variabilis* (Ide & Abe 2016).

Gall location and structure. Sexual unicolular (sometimes several galls) are on young acorn cup. Galls are pale green or brownish green, oval, pointed at apex, with one larval chamber, 2.0 mm in diameter, 4.0 mm in height, covered with dense, short, white pubescence. Asexual galls, usually one to three galls, are on a leaf petiole; galls are pinkish red or blackish purple, oval, containing one larval chamber, 1.0–1.5 mm in diameter, 1.5–2.0 mm in height (Yukawa & Masuda 1996, Ide & Abe 2016).

Phenology. The life cycle was described by Yukawa and Masuda (1996). The sexual generation galls appear in late April and mature in mid-May; adults emerge in mid- or late June and females lay eggs in the petioles of young leaves. The galled petioles begin to thicken in early July. The asexual generation galls appear from mid-July to September and mature in 7–10 days after their appearance. The mature galls fall to the ground; adults emerge from following March and lay eggs in juvenile acorns (Ide & Abe 2016).

***Latuspina hellwegi* (Dettmer, 1934)**

Synonyms: *Neuroterus hellwegi* Dettmer, 1934; *Latuspina hellwegi*: Ide & Abe (2016).

Lifecycle. Alternating sexual and asexual generations are known (Ide & Abe 2016).

Geographic distribution. Japan (Honshu, Shikoku, Kyushu) (Yukawa & Masuda 1996).

Host plants. *Quercus acutissima* for both generations (Ide & Abe 2016).

Gall location and structure. The sexual generation galls are at the base of male flowers; yellowish green or brown, spindleshaped, pointed at apex, containing one larval chamber, 1.5–2.0 mm in diameter, 3.0–4.0 mm in height, polished, smooth with pubescence at apex. Asexual generation unilocular galls are on the upper and lower sides of leaf vein, mainly midrib; horn-shaped, pointed at the apex, containing one larval chamber, 1.5 mm in diameter, 2.5–4.0 mm in height, with several vertical shallow striae on the surface. Immature galls green, mature ones yellowish green.

Phenology. The life cycle was described by Yukawa & Masuda (1996). The sexual generation galls begin to grow just before the buds burst and mature in mid-April; adults emerge from mid- to late April. The asexual generation galls begin to appear from mid-May and mature in 7–10 days after their appearance. After maturation, they fall to the ground from late May to late June. The asexual generation adults emerge in September of the same year (ide & Abe 2016).

***Latuspina kofuensis* Ide & Abe, 2016**

Lifecycle. Alternating sexual and asexual generations are known (Ide & Abe 2016).

Geographic distribution. Japan (Honshu, Shikoku, Kyushu), the Korean Peninsula (Yukawa & Masuda 1996).

Host plants. *Quercus acutissima* (Ide & Abe 2016).

Gall location and structure. The sexual generation galls are on leaf vein; pale green, oval, containing one larval chamber, 1.0–1.5 mm in diameter, 1.5–2.0 mm in height, covered with dense, gray white fine pubescence; the galled leaf distorted. The asexual generation unilocular galls are on midrib of both the upper and lower sides of leaf; yellowish white, pale green, yellowish red, or brown, oval, containing one larval chamber, 1.5–2.0 mm in diameter, smooth, polished (Ide & Abe 2016).

Phenology. The life cycle was described by Yukawa & Masuda (1996). The sexual generation galls appear in late April; adults emerge in mid-May. The asexual generation galls appear from late August to late fall and mature in about 10 days after their appearance. The mature galls fall to the ground; adults from late March to early April of the following year (Ide & Abe 2016).

***Latuspina manmiaoyangae* Melika & Tang, 2012**

Lifecycle. Only the sexual generation is known (Tang *et al*. 2012a).

Geographic distribution. Taiwan (Taoyuan and Nantou Counties, Taichung City) (Tang *et al*. 2012a).

Host plants. *Quercus variabilis* (Tang *et al*. 2012a).

Gall location and structure. Galls start to develop on young leaves. They are oval, purplish, hairy, 2.5–3.0 mm long and 1.4–1.8 mm wide. Galls protrude mainly on the lower leaf surfaces. Galls are single chambered with soft and juicy tissues surrounding the larval chambers of the young that turn hollow when the larvae mature (Figs A176–177) (Tang *et al*. 2012a).

Phenology. Galls start to grow in mid-February; adults emerge from late February until mid-March (Tang *et al.* 2012a).

***Latuspina nawai* (Ashmead, 1904)**

Synonyms: *Neuroterus nawai* Ashmead, 1904; *Latuspina nawai*: Ide & Abe (2016).

Lifecycle. Alternating sexual and asexual generations are known (Ide & Abe 2016).

Geographic distribution. Japan (Honshu, Shikoku, Kyushu) (Yukawa & Masuda 1996).

Host plants. *Quercus acutissima* and *Q. variabilis* for both generations (Ide & Abe 2016).

Gall location and structure. The sexual generation galls on vein on the lower side of leaf; yellowish white, oval, containing one larval chamber, 2.5–3.0 mm in diameter, 2.0 mm in height, covered with dense, white fine pubescence. The asexual generation galls are attached to midrib on lower side of leaf; each gall yellowish brown with brown scattered spots, oval or oblate, containing one larval chamber, 2.5 mm in diameter, 2.0 mm in height, matte (Ide & Abe 2016).

Phenology. The life cycle was described by Yukawa & Masuda (1996). The sexual generation galls mature in early May and fall to the ground. The sexual generation adults emerge from the galls from early to mid-May. The asexual generation galls appear from late July; mature asexual generation galls fall to the ground from early August to late October; adults emerge the following spring (Ide & Abe 2016).

***Latuspina shaanxinensis* Wang, Pujade-Villar & Guo, 2016**

Lifecycle. Only the sexual generation is known (Wang et al. 2016b).

Geographic distribution. China: Shaanxi, Houzhenzi (Wang et al. 2016b).

Host plants. *Quercus* sp. (Wang et al. 2016b).

Gall location and structure. An integral, almost discoid leaf gall swelling locates on leaf midrib with irregularly shaped, single larval chamber. Mature galls brown, up to 1.5 mm in diameter (Wang et al. 2016b).

Phenology. Galls are appearing on the tree from early May, developing and maturing through the summer and early autumn. Under the laboratory conditions, adults emerge from late September (Wang et al. 2016b).

***Latuspina stirps* Monzen, 1954**

Synonyms: *Neuroterus* (*Latuspina*) *stirps* Monzen, 1954. *Latuspina stirps*: Melika *et al*. (2010).
Lifecycle. Alternating sexual and asexual generations are known (Ide & Abe 2016).
Geographic distribution. Japan (Honshu, Kyushu) (Monzen 1954, Melika *et al.* 2010, Ide & Abe 2016), South Korea (Melika *et al.* 2010, Ide & Abe 2016).
Host plants. *Quercus acutissima* for both generations (Monzen 1954, Ide & Abe 2016).
Gall location and structure. The sexual galls are on the bark; gregarious, small subspherical galls (3–4 mm high and 2.0–2.5 mm in diameter), protruding from underneath the bark (Fig. A178) (Monzen 1954, Ide & Abe 2016). The asexual generation galls usually clustered into two to four galls on the midrib on the upper side of leaf; each gall is oval, containing one larval chamber, 1.5–2.0 mm in diameter, covered with thorns. Young gall is green, mature one pinkish-red or red-brown (Ide & Abe 2016).
Phenology. The sexual generation galls appear in early April and mature in late April; adults emerge from mid- to late May, and the females lay eggs in the midribs of young leaves. The asexual generation galls appear from late July to September; the mature galls begin to fall to the ground in mid-August; the asexual generation adults emerge from December to the following February and lay their eggs in stunted winter buds or latent buds (Ide & Abe 2016).
Comments. Sequences of three molecular markers (cytb, ITS2, D2 28S region) showed to be identical with those obtained for *N. hakonensis,* thus *L. stirps* might be well the alternate sexual generation of *N. hakonensis* (unpublished data).

Neuroterus Hartig, 1840

***Neuroterus abdominalis* Pujade-Villar & Wang, 2016**

Lifecycle. Only the asexual generation is known (Pujade-Villar *et al*. 2016).
Geographic distribution. China (Zhejiang) (Pujade-Villar *et al.* 2016).
Host plants. *Quercus acutissima* (Pujade-Villar *et al*. 2016).
Gall location and structure. Ox horn-shaped, unilocular galls on the main or lateral veins of leaf. The galls are 1.5– 2.0 cm long, milk white young galls turning to yellowish green and hollow with a hard and thin woody wall 2.0–2.5 mm thick when they become mature, and inside the interior space contains a single and free larval chamber (Pujade-Villar *et al*. 2016).
Phenology. Galls mature in September; adults emerge next year in early March (Pujade-Villar *et al*. 2016).

***Neuroterus gemma* Monzen, 1954**

Synonyms. Yukawa & Masuda (1996) suggested that this species is an inquiline, however, based on the description given by Monzen (1954) it is definitely *Neuroterus*.
Lifecycle. Only the asexual generation is known (Monzen 1954).
Geographic distribution. Japan (Monzen 1954).
Host plants. *Quercus serrata, Q. dentata* (Monzen 1954).
Gall location and structure. The leaf gall attached by a short petiole to the underside of leaf.

Galls are small, subspherical, smooth, yellowish or reddish in color, separable, unilocular, 5 mm in diameter, larval chamber small, in the innerside above the petiole (Monzen 1954).
Phenology. Galls matue in late autumn; adults emerge next year in April-May (Monzen 1954).

***Neuroterus haasi* Kieffer, 1904**
Lifecycle. Only the asexual generation is known
Geographic distribution. India (Bengal, Kurseong) (Kieffer 1904, Dalla Torre & Kieffer 1910, Mani 2000).
Host plants. In current classification, *Quercus spicata* Smith, which from this cynipid species was described, has been synonymized to *Lithocarpus elegans* (Blume) (Govaerts & Frodin 1998).
Gall location and structure. Induces gregarious blister-like galls on very young shoots (Kieffer 1906, Dalla Torre & Kieffer 1910).
Comments. Originally the species was assigned to *Neuroterus* (Kieffer 1904). However, the presence of an indistinct suture between the mesoscutum and mesoscutellum could also place the species into *Dryocosmus*. Whether *Neuroterus haasi* belong to *Drycosmus* or *Neuroterus* must be examined in details, including molecular sequence analysis.

***Neuroterus hakonensis* Ashmead, 1904**
Lifecycle. Only the asexual generation is known (Monzen 1954).
Geographic distribution. Japan (Monzen 1954).
Host plants. *Quercus acutissima* (Monzen 1954).
Gall location and structure. Small unilocular, kidney-shaped leaf gall attaches along the midrib of the underside (rarely upperside) of the leaf, small, oblong, yellowish, smooth, with thin, hard wall, 2 mm in length (Fig. A70) (Monzen 1954).
Phenology. Adults emerge in July (Monzen 1954).
Comments. Sequences of three molecular markers (cytb, ITS2, D2 28S region) showed to be identical with those obtained for *L. stirps*, thus *N. hakonensis* might be well the alternate asexual generation of *L. stirps* (unpublished data).

***Neuroterus moriokensis* Monzen, 1954**
Lifecycle. Alternating sexual and asexual generations are known (Yukawa & Masuda 1996). The sexual generation was described by Monzen (1954), later Yukawa & Masuda (1996) established the asexual generation.
Geographic distribution. Japan (Monzen 1954).
Host plants. *Quercus mongolica* subsp. *crispula, Q. serrata* (Monzen 1954).
Gall location and structure. Sexual generation catkin galls are small, irregular in shape, yellowis brown, covering with very short hairs, about 2 mm (Monzen 1954). The asexual generation galls are in buds (Figs A179–180).
Phenology. Sexual generation catkin galls mature in May; adults emerge in May (Monzen 1954).

***Neuroterus orbis* Monzen, 1954**
Lifecycle. Only the sexual generation is known (Monzen 1954).
Geographic distribution. Japan (Monzen 1954).
Host plants. *Quercus serrata* (Monzen 1954).

Gall location and structure. Leaf gall, sprouting small young leaf becomes gall which is rounded, brownish, 2–3 mm in diameter, unilocular, with sparse surface hairs (Fig. A181) (Monzen 1954).
Phenology. Adults emerge in June (Monzen 1954).

Neuroterus sculpturatus **Pujade-Villar & Wang, 2016**
Lifecycle. Only the sexual generation is known (Pujade-Villar *et al*. 2016).
Geographic distribution. China (Shaanxi) (Pujade-Villar *et al.* 2016).
Host plants. *Quercus variabilis* (Pujade-Villar *et al*. 2016).
Gall location and structure. Galls in clusters on the leaf edge, with 3–5 galls in each cluster; individual galls are soybean-shaped, 0.5–1.0 cm in diameter. Young galls are integral and pale green, becoming dark green, and turning brown and detachable when mature. Individual galls are hollow-like, with a tough and thin woody 3.0–4.0 mm thick wall; the interior space with a single, free-rolling larval chamber (Pujade-Villar *et al*. 2016).
Phenology. Galls mature in mid-May; adults emerge in early June (Pujade-Villar *et al*. 2016).

Plagiotrochus Mayr, 1881

Plagiotrochus follioti **Pujade-Villar & Melika, 2009**
Lifecycle. Only the asexual generation is known (Melika *et al*. 2009).
Geographic distribution. Nepal (Phulcoki and Siwapuri Dara, 2600 and 2450 m a.s.l., respectively) (Melika *et al*. 2009).
Host plants. Unknown.
Gall location and structure. Unknown.
Phenology. Aduls were collected in October (Melika *et al.* 2009).

Plagiotrochus glaucus **Melika & Tang, 2011**
Lifecycle. Only the asexual generation is known (Tang *et al*. 2011b).
Geographic distribution. Taiwan (Nantou County) (Tang *et al.* 2011b)
Host plants. *Quercus glauca* (Tang *et al*. 2011b).
Gall location and structure. The gall is a swelling of branches and twigs, usually located in the middle of the twig, never apically; sometimes swellings develop at joints of twigs. The gall is up to 6.0 cm long, 1.2–1.5 cm in diameter, coloured the same as the bark of twigs. When the gall mature, tissues hard, lignified. Larval chambers (up to 14 mm in length and 3–5 mm in diameter) arranged perpendicularly to main axis of gall, radiating from center of twig toward gall surface, reaching to 2–3 mm from surface (Figs A182–183) (Tang *et al*. 2011b).
Phenology. Galls mature in late October; adults emerge in the following spring (Tang *et al.* 2011b).

Plagiotrochus indochinensis **Abe, Ide, Konishi & Ueno, 2014**
Lifecycle. Only females are known (Abe *et al.* 2014b).
Geographic distribution. Vietnam (Lam Dong Province) (Abe *et al.* 2014b).
Host plants. *Quercus helferiana* A.DC. (*Quercus* subgenus *Cyclobalanopsis*) This plant species is considered to be the host plant because the holotype female was observed to insert its ovipositor into a young sprout of this evergreen oak (Abe *et al*. 2014b).

Gall location and structure. Unknown.
Phenology. Adults emerge in March (Abe *et al*. 2014b).

***Plagiotrochus masudai* Ide, Wachi & Abe, 2010**

Lifecycle. Alternating sexual and asexual generations are known **(**Yukawa & Masuda 1996).
Geographic distribution. Japan (Honshu, Shikoku, Kyushu) (Ide *et al*. 2010, Yukawa & Masuda 1996)
Host plants. *Quercus glauca* (Yukawa & Masuda 1996, Ide *et al*. 2010).
Gall location and structure. Asexual generation galls are in somewhat swollen twigs, with oval larval chambers inside, 1.0–1.5 mm in diameter and 2.5–3.0 mm in length each, aggregated but separated from one another by yellowish brown or brown wooden wall (Ide *et al*. 2010). Sexual generation galls are in buds, its apical end slightly curved, but almost indistinguishable from the healthy bud on the basis of the outline. One to five larval chambers, 2.0 mm in diameter each, separated from one another by brownish yellow, thin and firm wall at the base of bud and visible by removing bud scales (Ide *et al*. 2010).
Phenology. Adults of the sexual generation emerge in April; females wasp lays eggs in elongating shoots but galls are not induced in the first year. In the second year, the affected twigs become slightly swollen and the larvae develop in the latter half of the year. In May or June of the third year, the adults of the asexual generation emerge from the swollen twig and lay eggs in juvenile buds. The larvae then begin their development in summer and hibernate as larvae or pupae. In the spring of the fourth year, the adults of the sexual generation emerge from the bud galls and the cycle is repeated (Yukawa & Masuda 1996, Ide *et al*. 2010).

***Plagiotrochus semicarpifoliae* (Cameron, 1902)**

Synonyms. *Callirhytis semicarpifoliae* Cameron, 1902; *Plagiotriochus semicarpifoliae*: Bellido *et al.* (2000).
Lifecycle. Only the asexual generation is known (Cameron 1902, Bellido *et al*. 2000).
Geographic distribution. NW Himalayas (Bellido *et al*. 2000).
Host plants. *Quercus semecarpifoliae* Smith (Cameron 1902, Mani 2000).
Gall location and structure. Galls are in acorns (Cameron 1902).

***Plagiotrochus smetanai* Melika & Pujade-Villar, 2009**

Lifecycle. Only the asexual generation is known (Bellido *et al*. 2000, Melika *et al*. 2009).
Geographic distribution. Nepal (Phulcoki, 2600 m a.s.l.) (Melika *et al.* 2009).
Host plants. Unknown.
Gall location and structure. Unknown.
Phenology. Aduls emerge in October (Melika *et al.* 2009).

***Plagiotrochus tarokoensis* Tang & Melika, 2016**

Lifecycle. Only the sexual generation is known (Tang *et al*. 2016b).
Geographic distribution. Taiwan (Hualien County). The host-plant *Quercus tarokoensis* is endemic to Taiwan, so it is possible that *P. tarokoensis* also a Taiwanese endemic (Tang *et al*. 2016b).

Host plants. *Q. tarokoensis* Hayata (*Quercus* subgenus *Quercussection Cerris*) (Tang *et al*. 2016b).

Gall location and structure. Integral unilocular leaf galls. The gall is small, yellowish-white pimple on midribs or lateral veins of young leaves (Fig. A184). The mature gall is 1.6–2.6 mm in length, 0.8–1.0 mm in width (Tang *et al.* 2016b).

Phenology. Galls mature in late March; adults emerge in March (Tang *et al.* 2016b).

Trichagalma Mayr, 1907

Trichagalma acutissimae (Monzen, 1953)

Synonyms: *Aphelonyx acutissimae* Monzen, 1953; *Trichagalma acutissimae*: Melika *et al*. (2010); *Trichagalma glabrosa* Pujade-Villar, 2012 (synonym in Wang *et al*. (2016a)).

Lifecycle. Alternating sexual and asexual generations are known (Wang *et al*. 2016a).

Geographic distribution. Japan, China, South Korea, Taiwan (Yukawa & Masuda 1996, Melika *et al.* 2010, Pujade-Villar & Wang 2012).

Host plants. *Quercus acutissima*, *Q. variabilis* (Yukawa & Masuda 1996, Melika *et al*. 2010).

Gall location and structure. The asexual gall is spherical, smooth, 5.0–7.0 mm in diameter, pale yellow, red or brownish-red with minute bark spots, unilocular, with larval chamber in the center, located on veins of both sides of the leaf of (Yukawa & Masuda 1996; Fig. A69). The sexual galls, scattered or gathered, are on the bracts of staminate flowers in the central stem of inflorescences, especially on the apically-located staminate flowers. Each gall has a single larval chamber, almost spherical, 1–2 mm in diameter (Wang *et al*. 2016a).

Phenology: Asexual galls begin to appear in early June; asexual adults emerge in late November to December (Yukawa & Masuda 1996, Melika *et al*. 2010) and lay eggs in catkin buds; sexual adults emerge in spring (Wang *et al*. 2016a).

Trichagalma formosana Melika & Tang, 2010

Lifecycle. Only the asexual generation is known (Melika *et al*. 2010).

Geographic distribution. Taiwan (Taoyuan, Hsinchu, Taichung, Nantou Counties), Japan (Melika *et al.* 2010).

Host plants. *Quercus acutissima*, *Q. variabilis* (Melika *et al*. 2010).

Gall location and structure. Galls may be found singly or in groups, most commonly on lateral buds of young shoots. Solitary galls are almost spherical, while closely clustered galls may be deformed (Fig. A118). Old galls persist on the host tree (Melika *et al*. 2010). The gall when young is juicy, soft, covered with small raised tubercles, and green with purple spots on areas exposed to direct sunlight. The gall when mature reaches 15 mm in diameter, and is brown with a slightly irregular surface. The mature gall is hollow, with a tough woody wall 1.5–2.5 mm thick. The interior space contains a single larval chamber, attached to the wall by a stalk, which, however, dry out when the gall is mature. The larval chamber is ovoid, up to 6 mm in length, and has a tough but thin wall (Melika *et al*. 2010).

Phenology. Galls appear on the tree from early August; adults emerge in December or might overwinter in the gall and emerge in spring of the following year (Melika *et al*. 2010).

Trichagalma serratae (Ashmead, 1904)

Synonyms: *Dryophanta serratae* Ashmead, 1904; *Trichagalma drouardi* Mayr, 1907; *Trichagalma serratae*: Monzen (1929); *Neuroterus serratae*: Abe (2006); *Trichagalma serratae*: Melika *et al*. (2010).

Lifecycle. Alternating sexual and asexual generations are known (Abe 1992, 2006, Yukawa & Masuda 1996).

Geographic distribution. Japan (Honshu, Shikoku and Kyushu), China and South Korea (Abe 2006, Abe *et al*. 2007, Melika *et al*. 2010).

Host plants. *Quercus acutissima*, *Q. variabilis* (Melika *et al.* 2010).

Gall location and structure. Sexual generation gall is a single-chambered gall, irregularly globulous with a thin wall, smooth, tinged with yellow or red, on the surface of the catkins; solitary or several galls clustered per catkin; maximum diamtere 2–3 mm. The asexual gall usually is coalesced but often separate, roughly spherical, closely covered with spines, light green at the appearance, turning fulvous, 10–20 mm in diameter (Figs A185–186). The larval chamber single with an air space between this and the outer woody gall wall, ovoid, attached by its base to the gall wall, maximum 5 mm in diameter (Abe 2006).

Phenology. Sexual generation galls mature in April-May; adults emerge in May. Asexual galls appear in August; pupation take place in the following September. Some asexual larvae prolong their larval stage for one year (Yukawa & Masuda 1996).

Trigonaspis Hartig, 1840

Trigonaspis nephroideus (Kovalev, 1965)

Synonyms. *Neoneuroterus nephroideus* Kovalev, 1965; *Trigonaspis nephroideus*: Melika & Abrahamson (2002).

Lifecycle. Only the sexual generation is known (Kovalev 1965, Melika 2012).

Geographic distribution. Far East Russia (Kovalev 1965, Melika 2012).

Host plants. *Quercus dentata* (Kovalev 1965).

Gall location and structure. Galls are in buds. Infested buds usually enlarged, with 5-7 larval chambers inside (Kovalev 1965).

Phenology. Adults emerge in late May (Kovalev 1965).

Trigonaspis spumeus (Kovalev, 1965)

Synonyms. *Neoneuroterus spumeus* Kovalev, 1965; *Trigonaspis spumeus*: Melika & Abrahamson (2002).

Lifecycle. Only the sexual generation is known (Kovalev 1965, Melika 2012).

Geographic distribution. Russia (Far East) (Kovalev 1965, Melika 2012).

Host plants. *Quercus mongolica* (Kovalev 1965).

Gall location and structure. Juicy, spherical bud galls, 5–9 mm in dimeter, with 6 larval chambers in the center of the gall. Galls are green when growing, turn brown when mature. Usually on young sprouts (Kovalev 1965).

Phenology. Adults emerge in May (Kovalev 1965).

Trigonaspis vernicosus (Kovalev, 1965)

Synonyms. *Neoneuroterus vernicosus* Kovalev, 1965; *Trigonaspis vernicosus*: Melika & Abrahamson (2002).

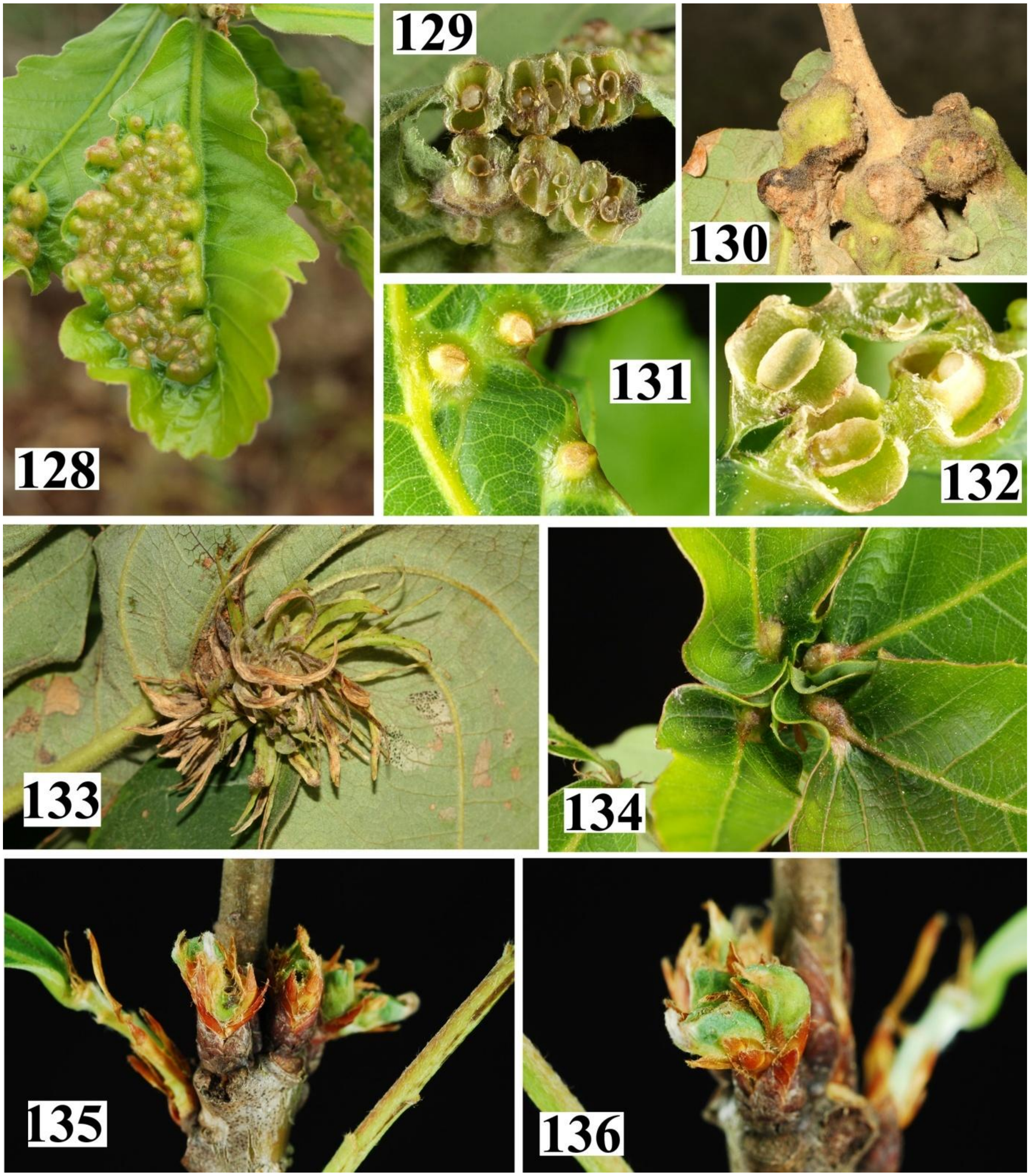
Lifecycle. Only the adult females are known (Kovalev 1965).

Geographic distribution. Russia (Far East) (Kovalev 1965, Melika 2012).
Host plants. *Quercus dentata* (Kovalev 1965).
Gall location and structure. Unknown.
Phenology. Females were caught ovipositing into buds (Kovalev 1965).

Ussuraspis Kovalev, 1965

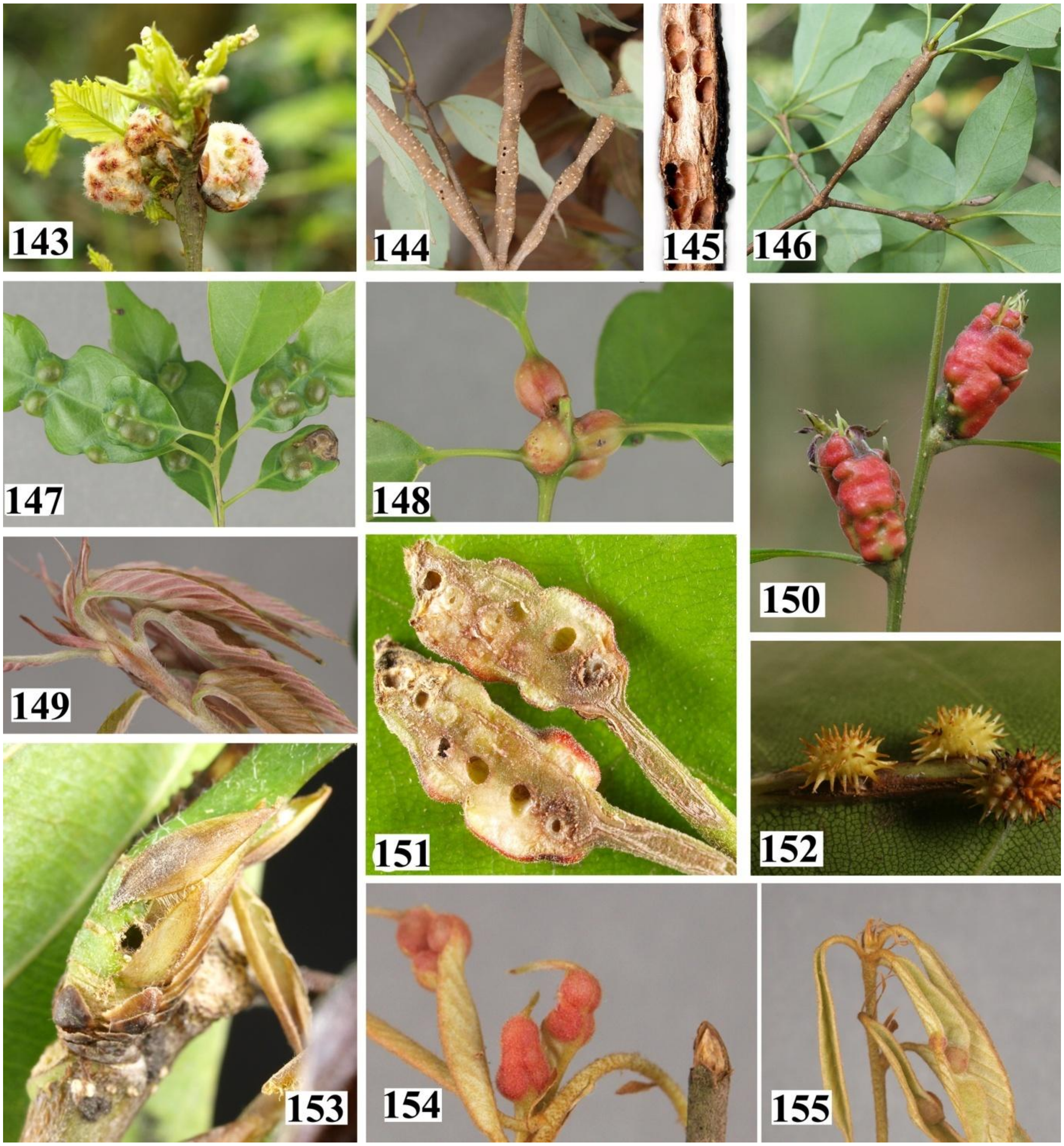
Ussuraspis nervosa Kovalev, 1965

Synonyms: *Ussuraspis nervosa* Kovalev, 1965; *Trigonaspis nervosus*: Melika & Abrahamson (2002); *Ussuraspis nervosa*: Melika (2012).
Lifecycle. Only the asexual generation is known (Kovalev 1965, Melika 2012).
Geographic distribution. Russia (Far East) (Kovalev 1985, Melika 2012).
Host plants. *Quercus mongolica* (Kovalev 1965).
Gall location and structure. Unilocular small shiny elongated leaf galls, often gregarious, attached to the split midrib along the gall's long axis (Figs A187–188); single galls located on the leaf edge usually are rounded, 2.0–3.5 mm in diameter (Kovalev 1965).
Phenology. Galls mature in August; adults emerge in December (Kovalev 1965).
Similar galls. Galls are similar to those induced by the asexual generations of the western-palearctic species, *Pseudoneuroterus saliens* (Kollar) and *Neuroterus anthracinus* (Curtis).

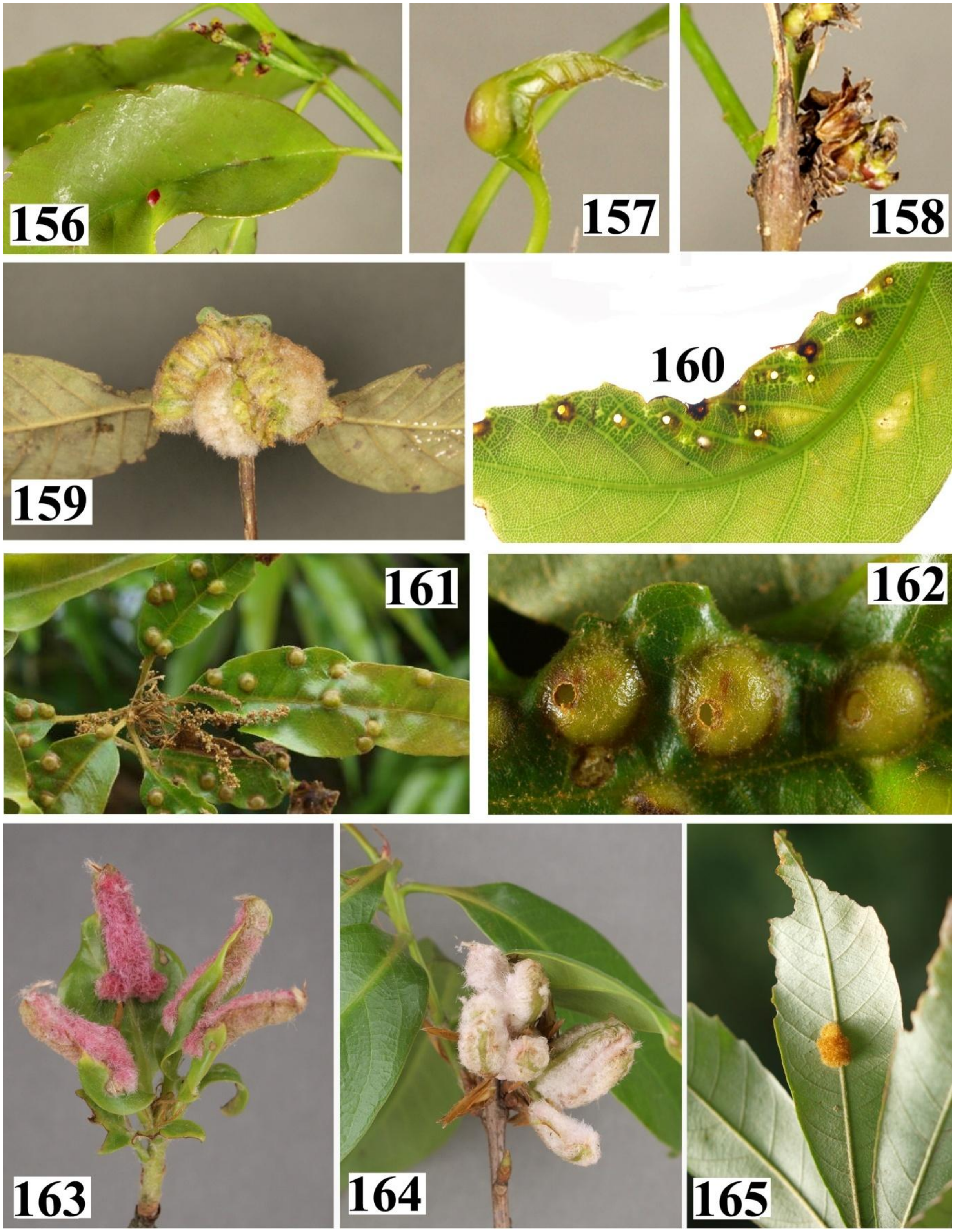


FIGURES A128–A136. Eastern Palearctic oak galls: 128–129, *Andricus formosanus*, sexual galls: 128, general appearance, 129, dissected galls with larval chambers. 130, *Andricus hakonensis*, sexual galls. 131–132, *Andricus pseudocurvator*, sexual galls: 131, general appearance, 132, dissected galls with larval chambers. 133, *Andricus pseudoflos*, asexual gall, 134–136, *Andricus songshui*, sexual galls: 134, galls on developed leaves, 135, 136, galls on bursting leaves.

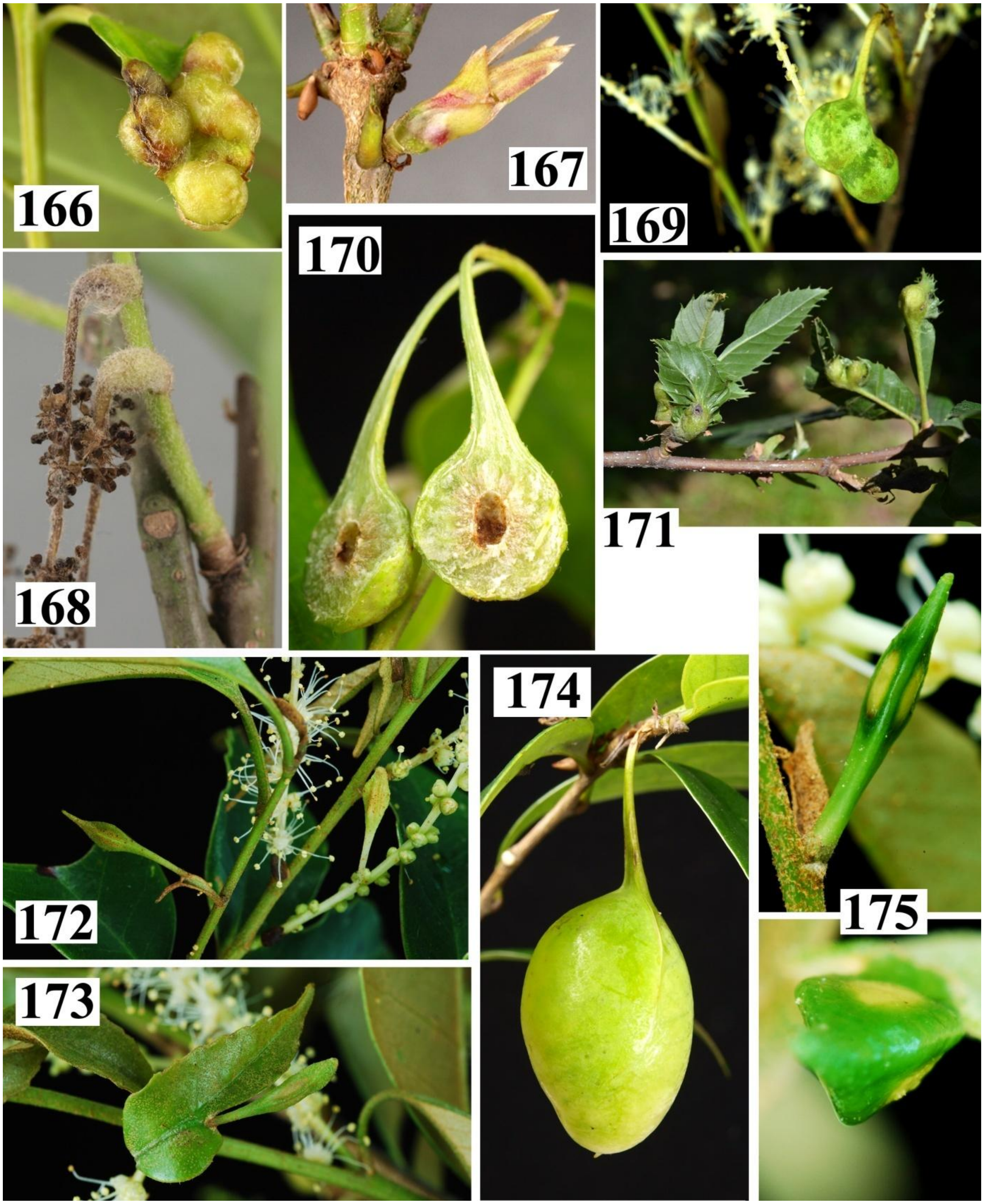
FIGURES A137–A142. Eastern Palearctic oak galls: 137–138, *Andricus xishuangbannaus*, sexual galls: 137, gall from upper side of leaf, 138, gall from under side of leaf. 139, *Belizinella gibbera*, asexual gall. 140, *Biorhiza nawai*, sexual gall. 141, *Callirhytis glanduliferae*, 142, *Cerroneuroterus folimargo*, asexual gall.



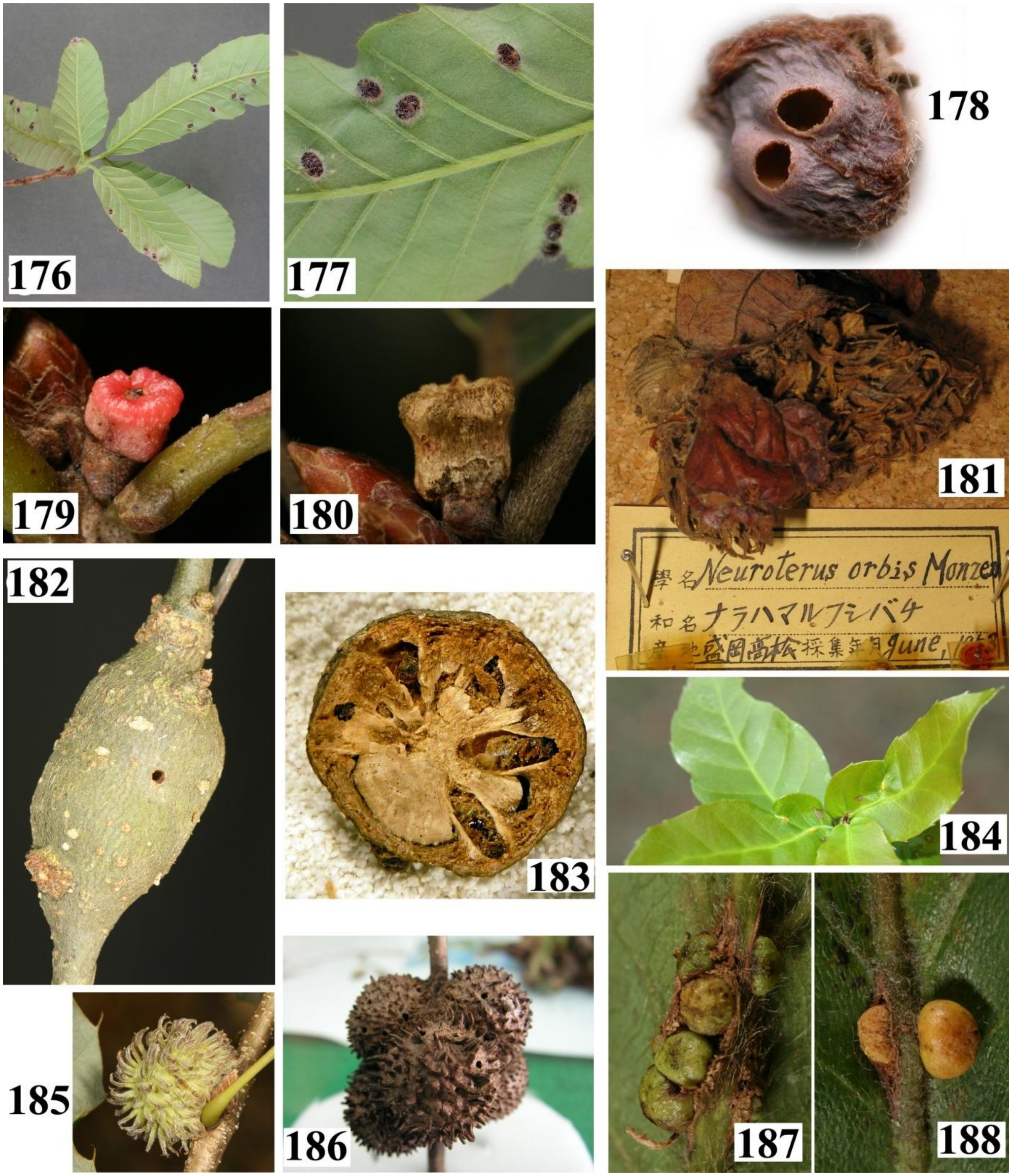
FIGURES A143–A155. Eastern Palearctic oak galls: 143, *Cerroneuroterus vonkuenburgi*, sexual galls, 144–145, *Cyclocynips uberis*, asexual gall: 144, general appearance, 145, dissected gall. 146, *C. tumorvirgae*, asexual gall, general appearance. 147–148, *Cycloneuroterus abei*, sexual galls. 149, *C. ergei*, sexual gall. 150–152, *C. formosanus*, sexual galls: 150, sexual gall, general appearance, 151, dissected sexual gall, 152, asexual galls. 153, *C. fortuitusus*, sexual gall. 154–155, *C. gilvus* sexual galls.



FIGURES A156–A165. Eastern Palearctic oak galls: 156–158, *Cycloneuroterus globosus*, sexual galls. 159, *C. jianwui*, sexual gall. 160, *C. lilungi*, sexual galls. 161–162, *C. lirongchiuea*, sexual galls. 163–165, *C. lohsei***:** 163–164, sexual galls, 165, asexual gall.



FIGURES A166–A175. Eastern Palearctic oak galls: 166, *Cycloneuroterus longinuxus*, sexual galls. 167, *C. tumiclavus*, sexual galls. 168, *C. uraianus*, sexual galls. 169–170, *Dryocosmus carlesiae*, sexual galls: 169, general appearance, 170, dissected gall. 171, *D. kuriphilus* asexual galls. 172–173, *D. pentagonalis*, sexual galls: 172, gall on catkin, general view, 173, gall on leaf. 174, *D. testisimilis*, sexual gall. 175, *D. triangularis*, sexual gall.



FIGURES A176–A188. Eastern Palearctic oak galls: 176–177, *Latuspina manmiaoyangae*, sexual galls: 176, general appearance, 177, close-up view. 178, *L. stirps*, sexual gall. 179–180, *Neuroterus moriokensis*, asexual galls: 179, young developing gall, 180, mature gall. 181, *N. orbis*, sexual gall (taken from Monzen collection). 182–183, *Plagiotrochus glaucus*, asexual gall: 182, general appearance, 183, cross-section of the gall. 184, *P. tarokoensis*, sexual generation gall. 185–186, *Trichagalma serratae*, asexual galls: 185, young developing gall, 185, mature galls. 187–188, *Ussuraspis nervosa*, asexual galls: 187, young developing galls, 188, mature galls.

9.3. Eastern Palearctic Cynipini species with uncertain status

Andricus noliquercicola Shinji, 1938. Status uncertain. Types lost; unplaced species known from Japan and South Korea (Abe *et al*. 2007).

Andricus testaceipes subsp. *japonicus* Monzen, 1953. Status uncertain. Only the sexual generation is known from Japan which induces leaf midrib swelling multilocular yellowish galls up to 5x8 mm, which are protruding on the underside of the leaves on *Q. serrata*; adults emerge in June (Monzen 1953). The galls resembles those of *Andricus testaceipes* Hartig, 1840 known from the Western Palearctic, however, the wasps differ from those of *A. testaceipes* and in fact the name was given basis solely on the similarity in gall structure (Monzen 1953). In the Monzen collection one female and one male *Andricus* were found. Both specimens belong to the *Andricus* genus. A new name must be given, however, this species might be well synonymic to *A. mukaigawae*, sexual generation; so types must be revised.

Aphelomyx [sic!] *crispulae* Mukaigawa, 1920. Status uncertain. Mukaigawa (1920a) described the morphology of sexual generation wasps and their galls on *Q. mongolica* subsp. *crispula* (= *Q. crispula*). On the basis of the adult's description the wasps are *Synergus* (inquilines) rather than *Andricus* (gall inducers). However, the descriptions are not detailed enough to make a definite conclusion. The type lost thus, we treat it as an unplaced species.

Aphelomyx [sic!] *glanduliferae* Mukaigawa, 1920. Status uncertain. Based on field observations, Mukaigawa (1920b) demonstrated that this species has alternating generations and described the sexual generation wasps and galls of both generations (see galls on pictures on C-127 and C-143 in Yukawa & Masuda (1996); C-127 is a bud gall, while C-143 is a detachable rounded leaf gall, both on *Q. serrata*. However, the described wasps are more *Synergus* than *Andricus* and Mukaigawa probably described an inquiline. However, the descriptions are not detailed enough to make a definite conclusion. The type lost thus, we treat it as an unplaced species

Callirhytis kunugicola Shinji, 1943. Status uncertain. Japan. The types lost. Unplaced species (Abe *et al*. 2007). In Yukawa & Masuda (1996) it is depicted on C-083. According to the photo, the gall looks like more a dipteran gall-midge rather than a gallwasp.

Callirhytis tobiiro Ashmead, 1904. Status uncertain. Japan. On the basis of the original description this species is not a *Callirhytis*; it is more an asexual female of *Andricus*. The type must be revised (Abe *et al*. 2007).

Dryophanta japonica Ashmead, 1904. Status uncertain. The type must be revised. Japan. Erroneously transferred to *Dryocosmus* (Melika & Abrahamson 2002). Described on the basis of a single female specimen. On the basis of the description this could be a *Cynips* sexual female.

Dryophanta brunneipes Ashmead, 1904. Japan. Described on the basis of two females from Japan; status uncertain (Ashmead 1904). The type must be revised.