Article

ZOOTAXA

Andricus forni Pujade-Villar & Nicholls n. sp., a new species of oak gallwasp from China (Hymenoptera: Cynipidae)

JULI PUJADE-VILLAR[1,6], YIPING WANG[2], VÍCTOR CUESTA-PORTA[1*], RUI GUO[3],
JAMES A. NICHOLLS[4] & GEORGE MELIKA[5]

[1]*Department of Animal Biology, Barcelona University, Barcelona 08028, Catalonia.*

[2]*College of Forest and Biotechnology, Zhejiang Agricultural and Forestry University, Lin'an 311300, China.*
✉ *wyp@zafu.edu.cn;* 🄳 *https://orcid.org/0000-0003-2027-9398*

[3]*Administration Bureau of Zhejiang Quigliangfeng National Nature Reserve, Lin'an, Zhejiang 311300, China.*
✉ *guruwos@126.com;* 🄳 *https://orcid.org/0000-0003-1239-8872*

[4]*CSIRO, Australian National Insect Collection, Clunies Ross Street, Acton, ACT 2601, Australia.*
✉ *james.nicholls@csiro.au;* 🄳 *https://orcid.org/0000-0002-9325-563X*

[5]*Plant Health Diagnostic National Reference Laboratory, National Food Chain Safety Office, Budaörsi u. 141–145, Budapest 1118, Hungary.* ✉ *melikageorge@gmail.com;* 🄳 *https://orcid.org/0000-0002-5204-6890*

[6]✉ *jpujade@ub.edu;* 🄳 *https://orcid.org/0000-0001-7798-2717*

[7]✉ *vcuesta@ub.edu;* 🄳 *https://orcid.org/0000-0002-6616-904X*

*Corresponding author

Abstract

A new sexual form of a gallwasp, *Andricus forni* Pujade-Villar & Nicholls **n. sp.**, is described from China (Zhejiang province) based on males, females and galls collected on *Quercus serrata*. Data on the morphology, diagnosis, distribution and biology of the new species are provided. Molecular data are also provided to support this species. A key to Asian *Andricus* gallwasp species with similar integral leaf galls is presented. Finally we discuss the taxonomic status of Asian *Andricus* making these integral leaf galls, including uncertainty on the validity of both *Andricus quercicola* and *A. marmoratus*.

Key words: Cynipidae, gallwasp, *Andricus*, key, biology, China

Introduction

Gallwasps (Hymenoptera: Cynipidae) constitute the largest radiation of gall-inducing organisms with approximately 1400 described species (Liljeblad & Ronquist, 1998; Ronquist, 1999; Ronquist *et al*., 2015). Most of the species occur in temperate areas of the Holarctic Region and induce galls on a range of host plants, while about 200 species are inquilines in galls induced by other Cynipidae (Ronquist *et al*., 2015) and rarely appear in some midges galls.

The cynipid gallwasp fauna of the Eastern Palaearctic and Oriental regions is poorly known (Abe et al., 2007; Tang *et al*., 2012). Only 15 valid species of *Andricus* are recognized from the Eastern Palaearctic, mostly from Japan and the Russian Far East (Pénzes *et al*., 2018; Ide *et al*., 2018; Pujade-Villar *et al*., 2020). In contrast, the number of *Andricus* species in the Western Palaearctic is greater, at about 80 (Melika, 2006; Tavakoli *et al*., 2008; Melika *et al*., 2011; Dinç *et al*., 2014; Mutun *et al*., 2014; Pujade-Villar *et al*., 2015 and others).

Herein we describe a new *Andricus* species from China, *A. forni* Pujade-Villar & Nicholls **n. sp.**, based on its sexual generation only. Galls induced by this new species are small, spherical and integral within the leaf lamina. This gall morphology is shared by many other sexual forms of *Andricus* in the Eastern Palaearctic (Pénzes *et al*., 2018; Ide *et al*., 2018): *Andricus formosanus* Tang & Melika, 2009; *A. marmoratus* Kovalev, 1965; *A. moriokae* Monzen, 1953; *A. mukaigawae* Mukaigawa, 1913; *A. pseudocurvator* Tang & Melika, 2011; *A. quercicola* Shinji, 1940; *A. songshui* Tang & Melika, 2011; *A. wuhanensis* Ide, Abe, Su & Zhu, 2018; and *A. xishuangbannaus* Melika & Tang, 2012. This similarity in gall morphology makes identification of these species difficult in the field, so we provide information, including a key, on the morphological diagnoses of this group of species, and discuss the validity of some species. We also place the new species into a molecular phylogeny of Asian *Andricus*.

Material and methods

The terminology of gallwasp morphology follows Liljeblad & Ronquist (1998) and Melika (2006). Abbreviations for forewing venation follow Ronquist & Nordlander (1989), and cuticular surface terminology follows Harris (1979). Measurements and abbreviations used herein are: F1–F13, first and subsequent flagellomeres; POL (post-ocellar distance), the distance between the inner margins of the posterior ocelli; OOL (ocellar-ocular distance), the distance from the outer edge of a posterior ocellus to the inner margin of the compound eye; LOL, the distance between posterior and frontal ocelli. The width of the forewing's radial cell is measured from the margin of the wing to the Rs vein.

The Cynipini species listed above are associated with the following host plant species, all within *Quercus* subgenus *Quercus* L.: *Q. dentata* Thunb., *Q. fabrei* Hance, *Q. griffithii* Hook. F & Thomson ex Miq., *Q. mongolica* var *grosseserrata* (Blume) Rehder & E.H.Wilson, *Q. serrata* Murray. (= *Q. glandulifera* Blume).

SEM pictures were taken by the first author using a field-emission gun environmental scanning electron microscope (FEI Quanta 200 ESEM) for high-resolution imaging with gold-coating the specimens. Optical images of the adult were taken by the third author using an Olympus SC30 camera, coupled to an Olympus U-CMAD3, adapted to a stereomicroscope Olympus SZX10 with multiple images stacked and processed using the program Helicon Focus 6.2.2.

The type material is deposited in collections at the University of Barcelona (UB; collection Juli Pujade-Villar, Catalonia) and Zhejiang Agricultural and Forestry University (ZAFU).

As well as demonstrating the morphological distinctiveness of this new species, we used DNA sequence data from the mitochondrial cytochrome *b* gene (cytb) to determine its relationships to 10 other Asian *Andricus* species, including six species discussed herein whose sexual generations also induce spherical integral leaf galls. This gene has been used successfully for distinguishing relationships among congeners in multiple other studies of cynipids (for example Cerasa *et al*., 2018; Nicholls *et al*., 2018; Nicholls & Pujade-Villar, 2020; Tang *et al*., 2020). New sequence data were generated for a 433 base pair section of cytb amplified from whole genomic DNA extracts obtained from between 1–5 individuals per species using methods described in Nicholls *et al*. (2010), and supplemented with previously published data (Genbank accessions KX683600, KX683602, KX683604 and KX683609 from Nicholls *et al*., 2017; accessions MT183619–MT183621 from Pujade-Villar *et al*., 2020).

Sequences were aligned using Muscle v3.8.31 (Edgar, 2004). First and second codon positions were combined into a single data partition as they contained only a small number of variable sites, then appropriate substitution models were determined using the software jModeltest v2.1.7 (Darriba *et al*., 2012) for the 1st+2nd partition as well as another partition containing only 3rd codon positions. These models were simplified if not all substitution types specified in the jModeltest output were actually present in the respective partition. Phylogenetic relationships were estimated using MrBayes v3.2.7a (Ronquist *et al*., 2012) using an independent HKY+I model for each partition and a strict clock model. Two independent runs were performed, each for 5 million generations and sampled every 2000 generations; this provided effective samples sizes >600 for each model parameter. A majority-rule consensus tree was calculated using samples taken from the final 2 million generations of both runs.

Results

Andricus forni Pujade-Villar & Nicholls n. sp.
urn:lsid:zoobank.org:act:C88FE778-168B-4094-BAC4-881F3D88AE7E
(Figs 1–5)

Type material. HOLOTYPE ♀: "Tianmushan, Lin'an District, Hangzhou City, Zhejiang Province" (white label); *Q. glandulifera*, (24.iv.2011) 27.iv.2011 (leg. Rui Guo) (white label); "Holotype ♀, *Andricus forni* **n. sp.** (desig. J. P-V)" (red label). Holotype is deposited at UB (JP-V col.). Paratypes: 40♂ & 40♀ (20♂ & 20♀ at UB; 20♂ & 20♀ at ZAFU) with the same labels as holotype.

Additional material examined. Same data as holotype, 91♂ & 37♀ (14♂ & 10♀ UB, remainder at ZAFU). Tianmushan, Lin'an District, Hangzhou City, Zhejiang Province, *Q. glandulifera* (24.iv.2011) 25.iv..2011: 10♂ & 7♀ (previously labeled as "*Dryocosmus* spp10" and *D. fabri* in litt. det Wang). Kaishan Old Hall Attractions in Tianmu Mountain, Zhejiang Province, 11.v.1999: 1♀. Elephant Trunk Hill, Lin'an, Hangzhou City, Zhejuang

Province, ex *Q. glandulifera* var. *brevipetiolata* Nakai, Shijun Wang leg. (6.iv.2013) 23.iv.2013: 4♂ & 9♀ (previously labeled as "*Dryocosmus* spp4" det Wang); same data (5.iv.2014) 28.iv.2014: 1♂ & 22♀; same data (6.iv.2013) 23–26.iv.2013: 2♀; (23.iv.2013) 6.v.2013: 1♀. Changhua Town, Lin'an District, Hangzhou City, Zhejiang Province, *Q. glandulifera*, (12.iv.2013) 16.v.2014: 4♀ (previously labeled as "*Dryocosmus* spp8" det Wang; the emergence date is a mistake, it should be 2013). Qingliangfeng, Lin'an District, Hangzhou City, Zhejiang Province, *Q. glandulifera*, (12.iv.2013) 2.v.2013: 1♀ (leg Jie, sample code 5132), 2♀ used for DNA; 21.iv.2015: 1♀ (leg. Jie 6191). Xiangbishan Lin'an District, Hangzhou City, Zhejiang Province, *Q. glandulifera*, (6.iv.2014) 23.iv.2014: 2♀ (leg. Jie, sample codes 5261, 5134).

Diagnosis. *Andricus forni* **n. sp.** most closely resembles *A. xishuangbannaus* and *A. moriokae* by having the head anteriorly black, except on and around clypeus which is brown; malar space with striae; female antenna with F1 at most 1.2x as long as F2 while male antenna with last flagellomere at most 2.0x as long as broad and F1 slightly curved and not swollen apically; mesoscutum completely smooth or delicately alutaceous to smooth, only with very few setae along notauli and in the lateral corners;prominent part of the ventral spine of the hypopygium at most 4.0x as long as broad. In *A. forni* **n. sp.,** lower face dark and strongly alutaceous to coriaceous, frons alutaceous, in females POL1.6x OOL, in males 2.0x OOL; female antenna with 12 flagellomeres (sometimes the suture between F11–F12 is incomplete but always visible), radial cell 3.5x as long as broad, central and lateral propodeal areas smooth, without wrinkles or rugae; lateral propodeal carinae complete, curved outwards posteriorly; galls on *Q. serrata*. In *A. xishuangbannaus*, only females are known, lower face light brown, smooth and shiny; frons smooth and shiny; central propodeal area with some irregular wrinkles and rugae, lateral propodeal area rugose, galls on *Q. griffithii*. Finally, *Andricus moriokae* differs from *A. forni* **n. sp.** by having a shorter POL in females (around 1.3x OOL), female antenna with 11 flagellomeres, the radial cell longer (4.1x as long as broad) and, in males, the lateral propodeal carinae are incomplete basally (ending at the level of dorsal propodeal margin).

Etymology. Named after Mr. Joaquim Forn i Chiariello.

Description.

FEMALE. Body length 1.1–2.0 mm, n = 21.

Color. Head, mesosoma and metasoma entirely and uniformly very dark brown to black; clypeus and mandibles brown, usually lighter than the rest of lower head (Fig. 5b); antenna light brown, last flagellomeres sometimes slightly darker; maxillary and labial palpi light yellow; tegula light brown; legs uniformly light brown, with coxae slightly darker at the base; ventral spine of hypopygium brown.

Head (Fig. 1a, 1c, 1d) smooth, with sparse white setae on lower face; 2.0x broader than long in dorsal view, 1.3x broader than high and slightly broader than mesosoma in anterior view. Clypeus trapezoid, emarginate, with a weak median incision ventrally, weakly alutaceous, with some setae; anterior tentorial pits, epistomal sulcus and clypeo-pleurostomal line distinct, deep. Gena delicately alutaceous, not broadened behind eye, as long as diameter of eye in lateral view; malar space with delicate striae extending towards compound eye without reaching margin of eye, 0.3x shorter than height of eye. Compound eyes slightly convergent ventrally. Transfacial distance only 1.3x wider than height of eye; diameter of antennal toruli greater than distance between them, distance between torulus and inner margin of eye nearly equal to diameter of torulus; lower face, including slightly elevated median area, delicately coriaceous to alutaceous, with white setae. Frons and vertex delicately alutaceous, with few setae; interocellar area and occiput coriaceous. POL 1.6x broader than OOL; OOL 1.1–1.3x longer than LOL and around 2.0x longer than length of lateral ocellus; all ocelli of same size and shape. Postocciput and postgena smooth, shiny, without setae; posterior tentorial pit large, deep, the area below impressed; height of occipital foramen nearly equal to height of postgenal bridge; hypostomal carina emarginate, continuing into postgenal sulcus.

Antenna (Fig. 2a–b) with 12 flagellomeres, F11 longer than F12 (suture between F12 and F11 rarely incomplete); 1.3x longer than head+mesosoma; pedicel longer than broad; F1 around 1.1x longer than F2, 1.9x longer than pedicel; F2–F12 progressively shorter; placodeal sensilla on F2–F12, absent on F1. Antennal formula: 15: 12(x10): 23: 20: 17: 17: 16: 16: 15: 15: 15: 13: 12: 18.

Mesosoma (Fig. 3a–c) 1.15x longer than high. Pronotum smooth, shiny, with delicate parallel striae and dense white setae laterally; propleuron shiny, alutaceous to smooth anteriorly, with delicately coriaceous central and basal area. Mesoscutum smooth, shiny, with some white setae in the anterior corners and beside notauli; 1.2x wider than long (greatest width measured across mesoscutum at level of base of tegulae). Notauli complete, deep, slightly converging at the posterior end; anterior parallel, parapsidal, median mesoscutal lines absent; parascutal carina reaching notauli. Mesoscutellum rectangular, uniformly dull rugose to coriaceous, as long as broad, overhanging metanotum;

circumscutelar carina usually well impressed; scutellar foveae distinct, transversely ovate, narrow, with smooth and shining bottom, with a very short coriaceous median carina separating foveae. Mesopleuron and speculum smooth, shiny, without setae except for dense patch of setae on posteroventral quarter of mesopleuron, with few impressed foveae along acetabular carina; dorsal axillar area smooth, shiny; axillula with dense white setae; lateral axillar area coriaceous, without setae, sometimes with a few rugae; subaxillular bar triangular, smooth, shiny, most posterior part broader than height of metanotal trough; metapleural sulcus reaching mesopleuron at almost half of its height. Metascutellum uniformly rugose-carinated, metanotal trough smooth, shiny, with dense short white setae; ventral impressed area shorter than height of metascutellum, smooth; central propodeal area smooth, shiny; lateral propodeal carinae strong, curved outwards in posterior third; lateral propodeal area smooth, rarely alutaceous, with a single ruga next to spiracle, with dense long white setae. Nucha with irregular wrinkles and rugae.
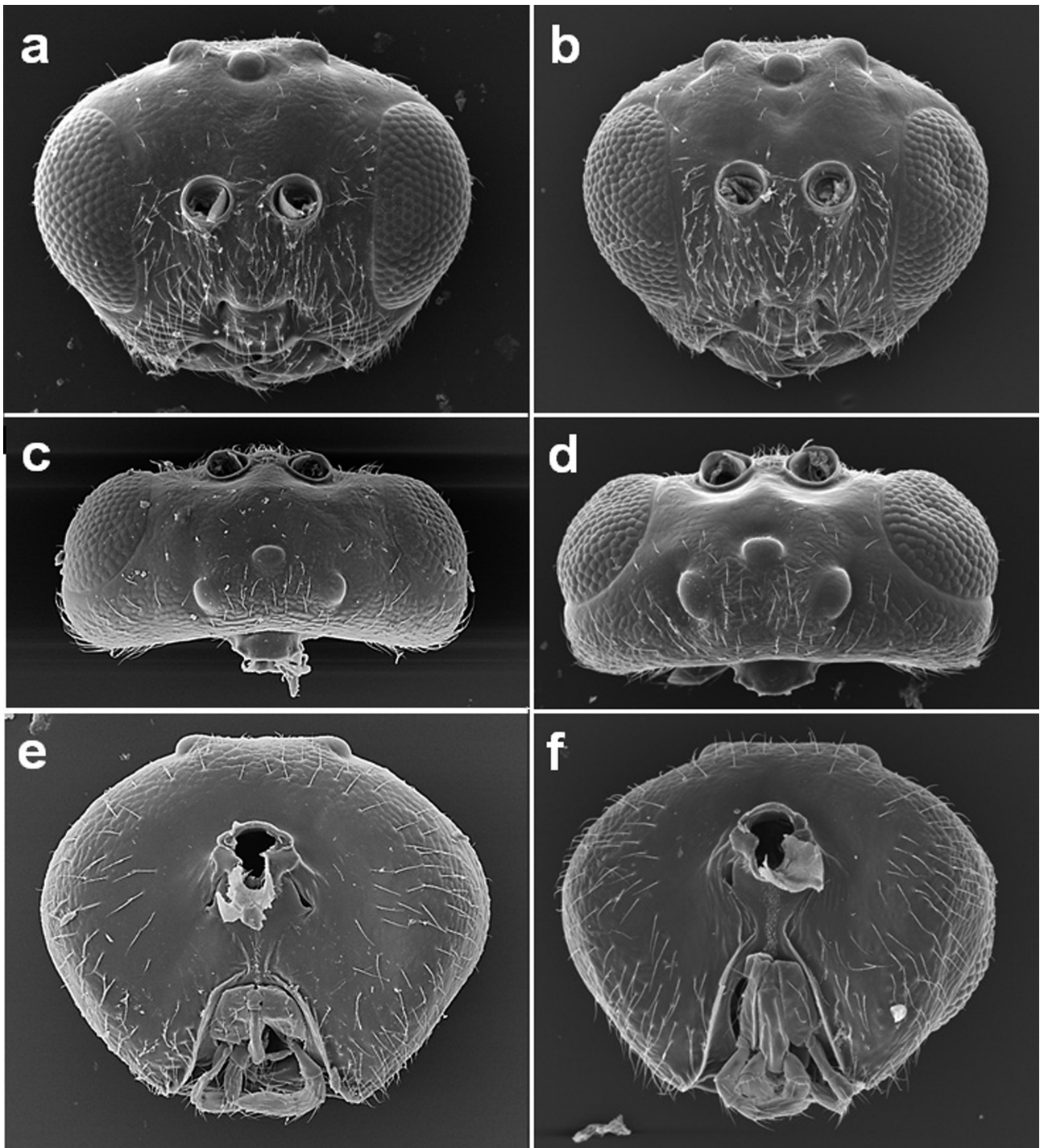

FIGURE 1. Head of *Andricus forni* **n. sp.**: (a) female in frontal view, (b) male in frontal view, (c) female in dorsal view, (d) male in dorsal view, (e) female in posterior view, (f) male in posterior view.
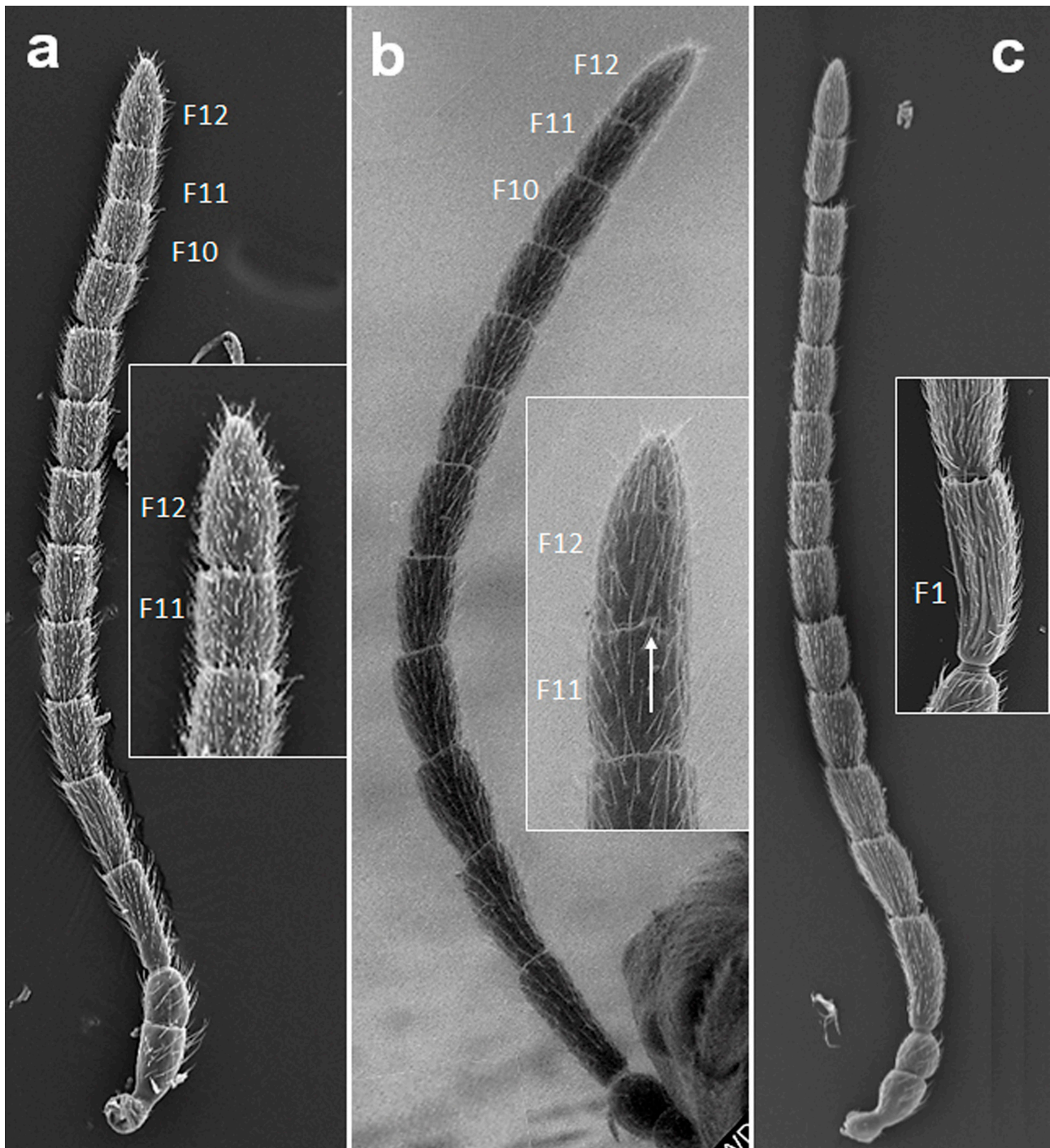
FIGURE 2. *Andricus forni* **n. sp.**, antennae: (a) female antenna with detail of last flagellomeres, F11 and F12 completely separated, b) female antenna with detail of last flagellomeres, F11 and F12 incompletely separated, (c) male with detail of F1.

Legs with tarsal claws with basal lobe.

Forewing (Fig. 5a) longer than body, hyaline, with distinct long, dense cilia on margin, radial cell 3.5x longer than wide; R1 reaching wing margin, Rs nearly straight, reaching wing margin; areolet small, triangular, closed and distinct. Rs+M distinct at two-thirds of distance to basalis and its projection reaching basalis at mid-height.

Metasoma (Fig. 4a) shorter than head+mesosoma, higher than long in lateral view; second metasomal tergite occupying more than half of metasoma in dorsal view, with some white setae laterally, all subsequent tergites without setae, smooth, shiny, with very delicate micropunctures. Hypopygium with micropunctures, ventral spine of hypopygium relatively short, prominent part 4.0x longer than broad, with two parallel rows of white setae ventrally.

MALE (Figs. 1b, 1d, 1f, 2c, 3d, 4b). Similar to female except for: clypeus with the same color as lower face (rarely lighter); middle of last femur and last tibia also slightly darker; malar space around 0.2x as long as height of eye; transfacial distance around 1.1x wider than height of eye; gena 0.5x shorter than cross diameter of eye in lateral view; POL about 1.9x broader than OOL; OOL subequal in length to lateral ocellus, and 1.3x longer than LOL; central ocellus smaller; antenna with 15 flagellomeres; pedicel as long as broad; F1 very slightly curved and not swollen apically, 1.3–1.4x longer than F2, 2.5–2.6x longer than pedicel and 3.8-4.3x as long as its narrowest width; F3–F12 subequal in length; F1–F6 slightly wider than the remainder of flagellomeres; placodeal sensilla on all flagellomeres; antennal formula: 10: 8(x8): 21: 15: 14: 14: 13: 13: 13. 13: 12: 12(x7): 12: 11: 15. Body length 1.0–1.6 mm, n = 15

Gall. The gall (Fig. 5c) is integral to the leaf blade, occurring singularly, never in clusters, without a distinct internal larval chamber. The gall is approximately spherical, 2.6–3.1 mm in height (n=6), and the outer gall tissues protrude equally on both sides of the leaf lamina.Young galls are fleshy, yellowish to green, turning dry and dark brown after emergence of the adult wasps.
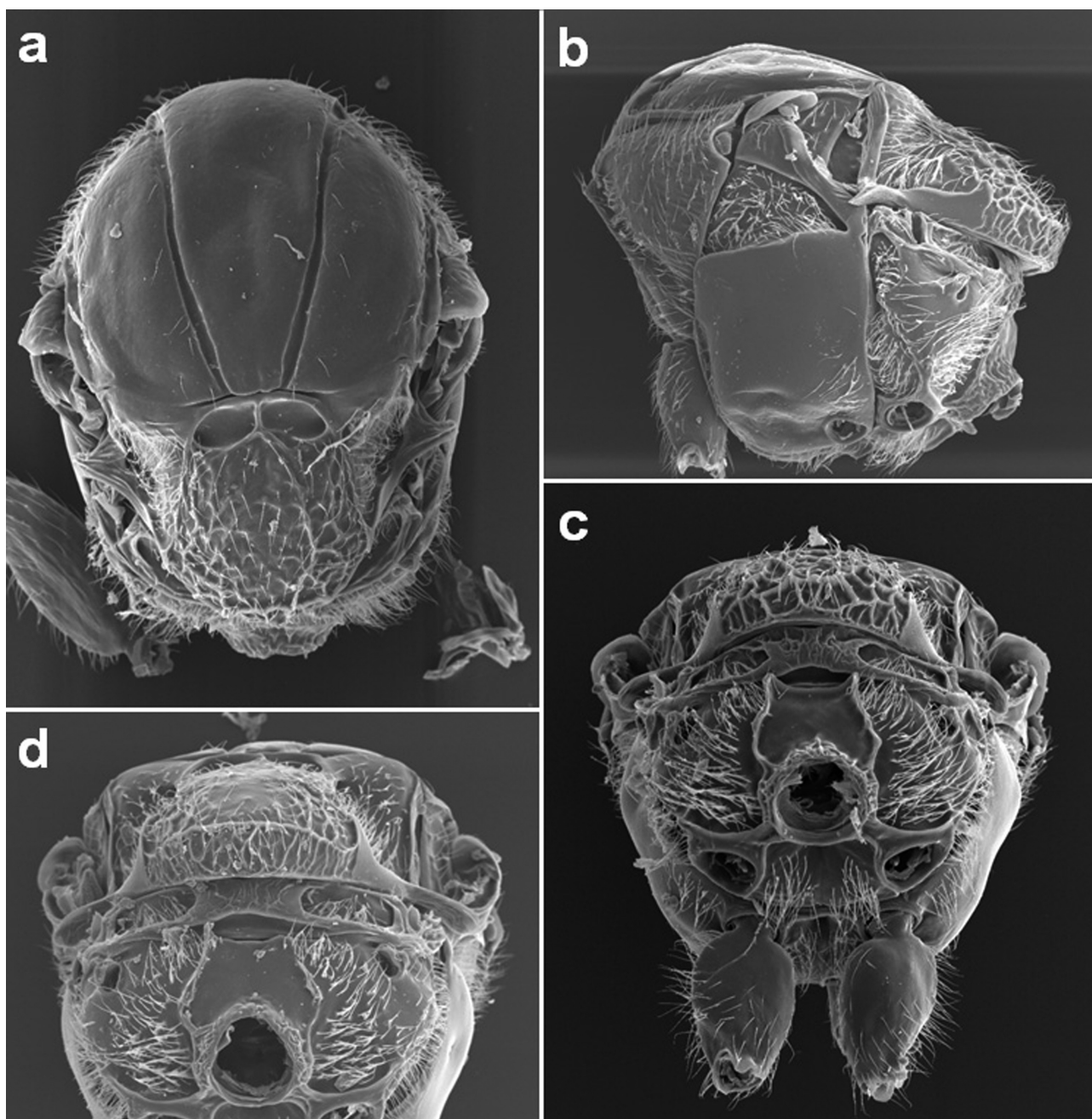

FIGURE 3. *Andricus forni* **n. sp.**, mesosoma: (a) female in dorsal view, (b) female in lateral view, (c) female propodeum, (d) male propodeum.
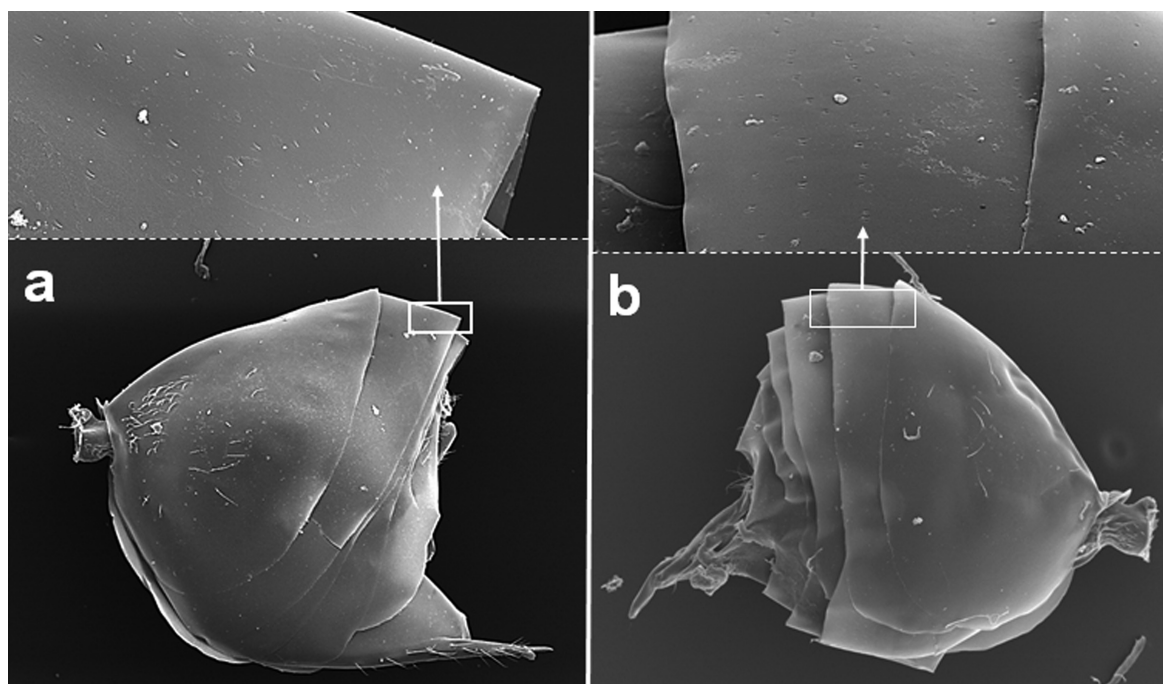
FIGURE 4. *Andricus forni* **n. sp.**, metasoma and details of micropunctures: (a) female, (b) male.

Biology. Only the sexual generation is known, inducing galls on *Q. serrata*. Mature galls were collected in mid-April, adults emerge from mid-April to May.

Distribution. Currently known only from Zhejiang Province, China. Probably distributed all over the range of its host plant. The host is native to southern, central and eastern China, also in Taiwan, Japan and Korea from 100 to 2000 m a.s.l. (Huang *et al*., 1999).

After a thorough examination of specimens and original descriptions of *A. pseudocurvator*, *A. songshui*, *A. formosanus* and *A. moriokae*, the descriptions of *A. mukaigawae*, *A. wuhanensis* and *A. xishuangbannaus,* the re-description of *A. moriokae*, and additional literature mentioned in the discussion, we propose the following key to differentiate the sexual generations of the valid *Andricus* species obtained from small spherical integral leaf galls on oaks in the Eastern Palaearctic and Oriental Regions. We also note the host oaks galled by each *Andricus* species.

1	Anterior half of mesoscutum distinctly sculptured, strongly alutaceous to coriaceous . . . . *A. songshui* [*Q. serrata*]	
-	Mesoscutum completely smooth or with a very delicate alutaceous or imbricate sculpture mainly in the anterior corners 2	
2	Mesoscutum obscurely imbricate with scattered hairs all over mesoscutum. Female F1 about 1.4x longer than F2 . . . . *A. mukaigawae* [*Q. serrata*, *Q. mongolica* var *grosseserrata*, *Q. dentata*]	
-	Mesoscutum smooth or delicately alutaceous, with a few setae only along notauli and in the lateral corners, with glabrous areas. Female F1 shorter, at most 1.2x longer than F2 3	
3	Females 4	
-	Males 9	
4	Prominent part of ventral spine of hypopygium at least 6.0x longer than broad 5	
-	Prominent part of ventral spine of hypopygium at most 4.0x longer than broad 6	
5	Antenna with 11 flagellomeres (but the last sometimes with an indistinct suture, so appears as 12 flagellomeres); central propodeal area without or with few irregular delicate wrinkles . . . . *A. pseudocurvator* [*Q. serrata*, *Q. fabrei*]	
-	Antenna with 11 flagellomeres; central propodeal area with irregular wrinkles . . . . *A. wuhanensis* [*Q. fabrei*]	
6	Head brown anteriorly, especially lower face; malar space without striae, frons with distinct alutaceous sculpture . . . . *A. formosanus* [*Q. dentata*]	
-	Head black anteriorly, any brown restricted to clypeus and around clypeus, malar space with striae; frons smooth, shiny or very delicately sculptured 7	
7	Lower face and frons smooth and shiny; central propodeal area with some irregular wrinkles and rugae, lateral propodeal area rugose . . . . *A. xishuangbannaus*	

[*Q. griffithii*]

- Lower face and frons delicately alutaceous to coriaceous; central and lateral propodeal area smooth, without wrinkles and rugae 8

8 POL about 1.6x as long as OOL; antenna with 12 flagellomeres, sometimes the suture between F11-F12 is incomplete; radial cell 3.5x as long as broad . . . .*A. forni* **n. sp.**
[*Q. serrata*]

- POL only 1.3x as long as OOL; antenna always with 11 flagellomeres, never with suture in F11; radial cell 4.1x as long as broad . . . .*A. moriokae*
[*Q. serrata*]

9 Last flagellomere more than 2x as long as broad. . . . .*A. pseudocurvator*
[*Q. serrata, Q. fabrei*]

- Last flagellomere at most 2.0x as long as broad 9

10 F1 apically swollen; body brown . . . .*A. formosanus*
[*Q. dentata*]

- F1 more cylindrical, very slightly curved and not swollen apically; body predominantly black 10

11 POL around 2x as long as OOL; lateral propodeal carinae complete, curved outwards in posterior third . . . .*A. forni* **n. sp.**
[*Q. serrata*]

- POL around 1.6x as long as OOL; lateral propodeal carinae diverging ventrally and incomplete or inconspicuous basally, ending at level of dorsal propodeal margin . . . .*A. moriokae*
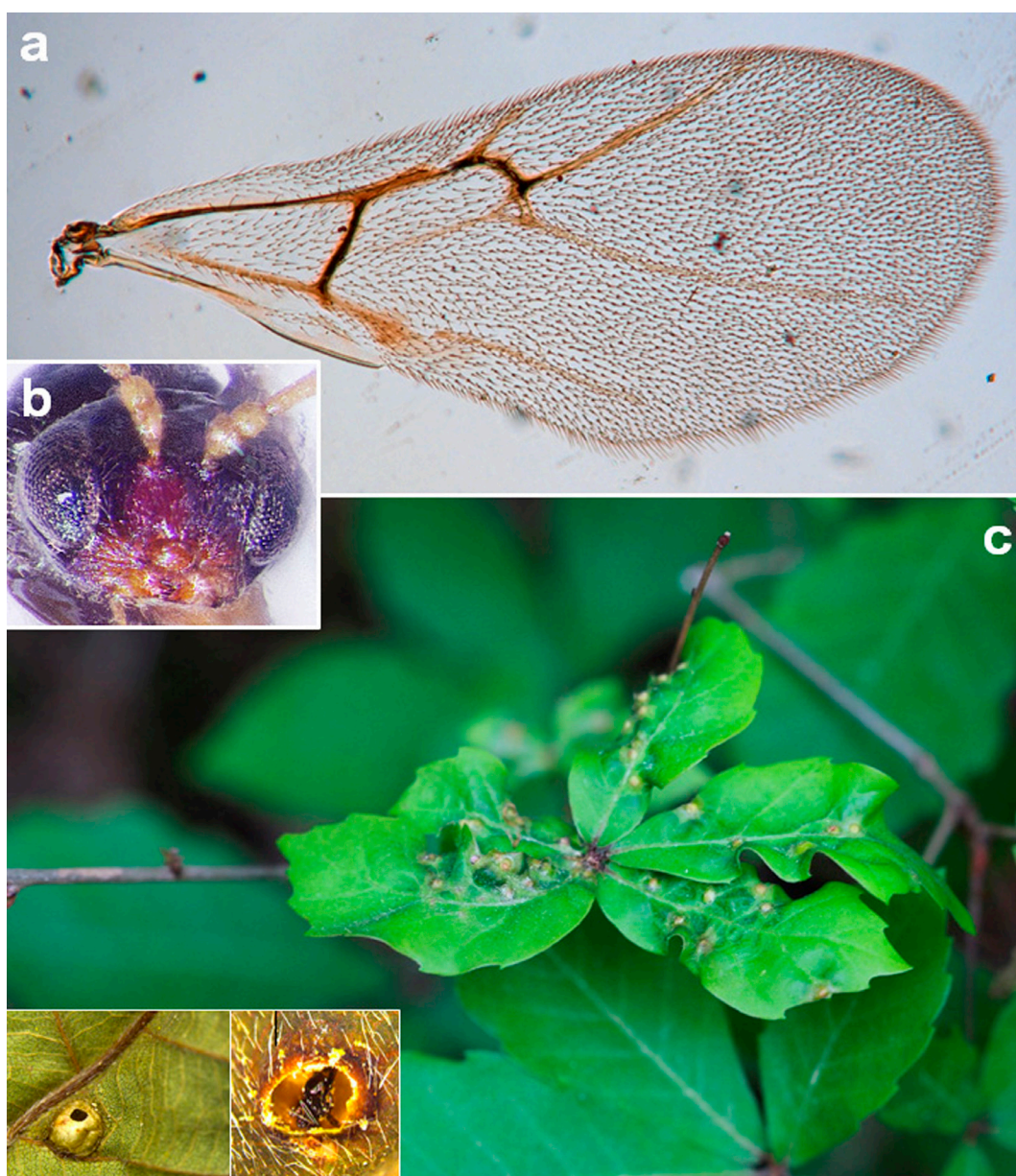[*Q. serrata*]

FIGURE 5. *Andricus forni* **n. sp.**: (a) forewing, (b) frontal head of female with clear area around clypeus, (c) galls with details.

The cytb tree of Asian *Andricus* contains four major clades indicated with A–D in Fig. 6. Major clades A, C and D contain species with sexual generations inducing integral leaf galls. The species *A. mukaigawae* is recovered as monphyletic in a well-supported node, sister to the terminals of *A. kashiwaphilus* and *A. pseudoflos*, albeit the internal relationships between these two species is not well resolved. The new species, *A. forni*, is recovered as monophyletic within the clade C, closely allied to *A. xishuangbannaus*, *A. moriokae*, *A. pseudocurvator* and *A. formosanus*, as is also suggested by the morphological similarity of *A. forni* with this group, in particular with the first two species. Within this group, *A. formosanus* is the most phylogenetically distinct, while the remaining four form a genetically close complex of species. However, these four still show divergence consistent with being discrete species; for example the new species *A. forni* is 1.7–2.5% divergent from the other three species, within the range observed for other distinct cynipid species (Nicholls *et al.*, 2018; Nicholls & Pujade-Villar, 2020). Finally, the species *A. hakonensis* and *A. songshui* are recovered within the clade D, which is sister to the rest of *Andricus* species, albeit the relationships between these two species is unclear. All new sequences are deposited in GenBank, accessions MT922013–MT922034.

Discussion

The group of Asian *Andricus* species whose sexual generations induce integral leaf galls is very complex morphologically and phylogenetically. It currently includes *A. formosanus*, *A. forni* **n. sp.**, *A. marmoratus*, *A. moriokae, A. mukaigawae, A. pseudocurvator, A. quercicola, A. songshui, A. wuhanensis,* and *A. xishuangbannaus*. Although, the morphological resemblance of the adults and some unclear phylogenetic relationships between species may indicate that there are more species than currently are known. Two different gall morphologies can be distinguished in this group of species: (i) those with an internal larval chamber separated from the surrounding gall tissues when mature (*A. formosanus, A. moriokae, A. pseudocurvator and A. wuhanensis*) and (ii) those in which the larval chamber is completely fused to the remainder of the gall, thus lacking the visibly isolated larval chamber (*A. forni* **n. sp.**, *A. mukaigawae, A. songshui* and *A. xishuangbannaus*). The galls of *A. quercicola* and *A. marmoratu*s, described respectively by Shinji (1940) and Kovalev (1965), are not sufficiently well described to assign them to either of these two gall types. Below we discuss this group of species, with comments on their taxonomy and distinguishing characteristics.

The set of species *A. forni* **n. sp.**, *A. moriokae* and *A. xishuangbannaus* is the most complex one within this group. The taxonomy of this complex has only been clarified relatively recently, with redescription of the type material of *A. moriokae* (from the oak host *Q. serrata)* by Ide *et al.* (2018) and establishment of the new species *A. xishuangbannaus* from *Q. griffithii* by Tang *et al*. (2012). We obtained multiple specimens (males and females; unlike *A. xishuangbannaus* which is known only from sexual females) from integral leaf galls collected from *Q. serrata*, attributable at first glance to *A. moriokae* which galls the same host oak. However, in some cases the morphology of the females also resembled that of *A. xishuangbannaus* (despite the different host), with a red coloured head around the mouthparts and the lower face and frons being smooth and shiny. The material collected by us was hence initially considered intermediate between *A. moriokae* and *A. xishuangbannaus*, perhaps suggesting that both species could be synonymous. We therefore performed molecular analyses to find out whether the genetics were consistent or not with possible synonymy. Given the levels of divergence among species (see Fig. 6), we concluded that our material corresponded to a new species, *A. forni* **n. sp.**, and further detailed study of the morphology of the three species revealed characters that could differentiate them (see below and our key).

Andricus xishuangbannaus (males unknown) differs from the other two species, in multiple characters, the most obvious being the lack of sculpture on the head (lower face and frons smooth in *A. xishuangbannaus* but delicately alutaceous to coriaceous in *A. forni* **n. sp.** and in *A. moriokae*) and by the oak host (*Q. griffithii* vs. *Q. serrata*). Both *Andricus moriokae* and *A. forni* **n. sp.** induce galls on *Q. serrata* leaves, but these species can be separated by the number of antennal segments in females (12 flagellomeres in *A. forni* **n. sp.**, 11 in *A. moriokae*) and by the propodeal carinae of males (complete and curved outwards in their posterior third in *A. forni* **n. sp.**, incomplete or inconspicuous in *A. moriokae*). We should also mention that the ratio of the last 4 flagellomeres of male mentioned in Ide *et al.* (2018: 820) is not taken into account to separate both species as it is surely a typographical mistake and inconsistent with the image they present of this species. We also note that *A. xishuangbannaus* is not the only species among the three mentioned in this complex to have very delicate micropunctures from the third metasomal

tergite onwards. This state is seemingly visible in *A. moriokae* (Ide *et al.*, 2018: Fig. 33), albeit not reflected in the re-description, and micropunctures are also present in *A. forni* **n. sp.** We suggest this character might contribute to defining this complex, and based on the genetic results hypothesise that it will be present in *A. pseudocurvator* and possibly also *A. formosanus*.

Andricus pseudocurvator is quite characteristic (Tang *et al.*, 2011) for a long ventral spine of the hypopygium in females (6.0x as long as broad), and very long antennal flagellomeres in males (more than 2.0x as long as broad). Ide *et al.* (2018) described *A. wuhanensis*, a species in which females have a very long ventral spine of the hypopygium and that induces galls identical to those of *A. pseudocurvator* although on a different host plant, *Q. fabrei*. The morphological differences that Ide *et al.* provided are very superficial (see our key) and after studying the respective species descriptions we cannot find any other differences, which suggests that these two species may be well synonymous. The males of *A. pseudocurvator* differ from all the other males of this species group by having longer flagellomeres, while no males are known in *A. wuhanensis*. Until males of *A. wuhanensis* are described, we cannot be sure whether these species are synonymous or not.

Andricus formosanus poses no apparent taxonomic problems (Tang *et al.*, 2009). We note that within the group of *A. forni* **n. sp.**, *A. moriokae*, *A. xishuangbannaus*, *A. pseudocurvator* and *A. formosanus* (clade C in Fig.6), an asexual generation is only described for *A. pseudocurvator*, inducing small oval galls on terminal buds (Ide *et al.*, 2018). However, recent DNA sequencing of larvae dissected from a similar gall induced on lenticel buds on *Q. dentata* in Taiwan shows this gall to be induced by the asexual generation of *A. formosanus*, although adults are yet to be reared (C.-T. Tang, pers. comm.).

Andricus songshui can be separated from all the other species of this group by the sculpture of the mesoscutum, as highlighted by Tang *et al.* (2011) who used this character in their key to *Andricus* species in Taiwan. This mesoscutal sculpturing is shared by *A. hakonensis* (see Fig. 6 of Wachi & Abe, 2010), consistent with the phylogenetic results presented in this study. We note that Fig. 19 of Tang *et al.* (2009) shows a sculptured mesoscutum for *A. moriokae*. After they examined the type material of *A. moriokae*, Ide *et al.* (2018) concluded that this species has a smooth mesoscutum. Thus, the specimen photographed as *A. moriokae* in Tang *et al.* (2009) is definitely not *A. moriokae* and might be well an undescribed species or an extreme variant of *A. songshui*.

The description of the sexual generation of *A. mukaigawae* is incomplete (Abe, 1986), and unfortunately misses important diagnostic characters. In spite of this, the only image that Abe (1986) presents and the configuration of female antennae allow us to distinguish this species from the other species of the group. *Andricus mukaigawae* has scattered hairs all over the surface of the mesoscutum, while in the remainder of the species in this group the mesoscutum is practically glabrous or with only a few setae beside the notauli or in the anterior corners. We also note that Abe's (1986) description predates the recognition of *A. kashiwaphilus* as a species distinct from *A. mukaigawae* (see Abe, 1998), hence this description could apply to either species. This is reinforced by the host range presented by Abe (1986) that includes both the oak host now known to be typical of *A. mukaigawae* sensu stricto (*Q. serrata*) and the only host of *A. kashiwaphilus* (*Q. dentata*). The phenology of the sexual generations of these two species is known to differ (Abe, 1991), but unlike their asexual generations (see Pujade-Villar *et al.*, 2016) no work has been done to establish any morphological diagnosis of sexual adults of these two close species.

Finally, the taxonomic status of two species in this group is uncertain. Regarding *A. quercicola*, Abe *et al.* (2007) mentioned that this is an unplaced species and the types have been lost. Later, Pénzes *et al.* (2018) erroneously considered this species as a valid one. The present study could not find the type material of this species. After reading the short description from Shinji (1940) and Monzen's (1953) re-description, it is impossible to distinguish this species from others with similar galls. Thus, *A. quercicola* Shinji, 1940 is considered herein as an *unplaced species*. Kovalev's (1965) description of *A. marmoratus* indicates that it might be a valid species closely resembling to *A. songshui*, having surface sculpturing on the anterior part of the mesoscutum. However, it presumably differs as the description says it has no propodeal carinae. This character is very unusual in the genus *Andricus*, thus we consider this species as *nomina dubia* until the types can be examined.
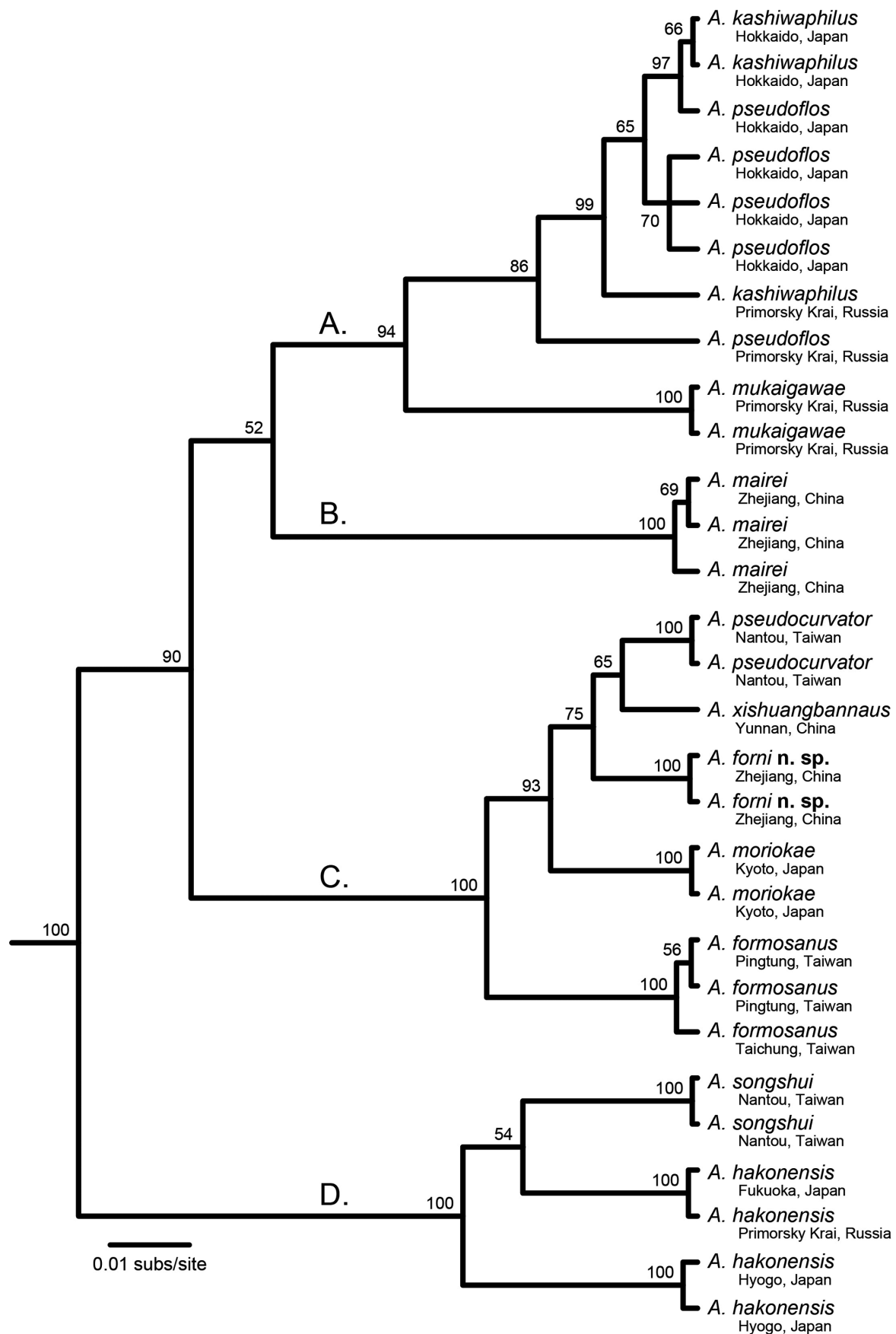
FIGURE 6. Bayesian majority-rule consensus tree of 433bp of cytochrome *b* sequence derived from Asian *Andricus* species. Numbers at nodes indicate posterior probability support; major clades mentioned in the text are indicated by the letters A–D.

Bibliography

Abe, Y. (1986) Taxonomic status of the *Andricus mukaigawae* complex and its speciation with geographical parthogenesis (Hymenoptera: Cynipidae). *Applied Entomology and Zoology*, 21, 436–447.
https://doi.org/10.1303/aez.21.436

Abe, Y. (1991) Host race formation in the gall wasp *Andricus mukaigawae*. *Entomologia Experimentalis et Applicata*, 58, 15–20.
https://doi.org/10.1111/j.1570-7458.1991.tb01446.x

Abe, Y. (1998) Karyotype differences and speciation in the gall wasp *Andricus mukaigawae* (s. lat.) (Hymenoptera: Cynipidae), with description of the new species *A. kashiwaphilus*. *Entomologica scandinavica*, 29, 131–135.
https://doi.org/10.1163/187631298X00249

Abe, Y., Melika, G. & Stone, G.N. (2007) The diversity and phylogeography of cynipid gallwasps (Hymenoptera: Cynipidae) of the oriental and Eastern Palearctic regions, and their associated communities. *Oriental Insects*, 41, 169–212.
https://doi.org/10.1080/00305316.2007.10417504

Cerasa, G., Lo Verde, G., Caleca, V., Massa, B, Nicholls, J.A. & Melika, G. (2018) Description of *Dryocosmus destefanii* new species (Hymenoptera: Cynipidae: Cynipini) from *Quercus suber* L. in Italy. *Zootaxa*, 4370 (5), 535–548.
https://doi.org/10.11646/zootaxa.4370.5.5

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9, 772.
https://doi.org/10.1038/nmeth.2109

Dinç, D., Mutun, S. & Melika, G. (2014) A new species of *Andricus* Hartig oak gall wasp from Turkey (Hymenoptera: Cynipidae, Cynipini). *North-Western Journal of Zoology*, 10 (1), 122–127.
https://doi.org/10.11646/zootaxa.3760.2.5

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797.
https://doi.org/10.1093/nar/gkh340

Huang, C., Zhang, Y. & Bartholomew, B. (1999) Fagaceae. *In*: Wu, Z.-Y. & Raven, P.H. (Eds.), *Flora of China. Vol. 4. Cycadaceae through Fagaceae*. Science Press, Beijing and Missouri Botanical Garden Press, St. Louis, pp. 314–400.
[on-line: http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=10338]

Harris, R. (1979) A glossary of surface sculpturing. *State of California, Department of Food and Agriculture, Occasional Papers in Entomology*, 28, 1–31.

Ide, T., Abe, Y., Su, C.Y. & Zhu, D.H. (2018) Three species of *Andricus* Hartig (Hymenoptera: Cynipidae) inducing similar galls in East Asia, with description of a new species and the asexual generation of *A. pseudocurvator*, and redescription of *A. moriokae*. *Proceedings of the Entomological Society of Washington*, 120 (4), 807–824.
https://doi.org/10.4289/0013-8797.120.4.807

Kovalev, O.V. (1965) Gall wasps (Hymenoptera, Cynipidae) from the south of the Soviet Far East. *Entomologicheskoye Obozrenije*, 44 (1/2), 46–73. [in Russian, English translation in *Entomological Review*, 44, 25–38]

Liljeblad, J. & Ronquist, F. (1998) A phylogenetic analysis of higher-level gall wasp relationships (Hymenoptera: Cynipidae). *Systematic Entomology*, 23, 229–252.
https://doi.org/10.1046/j.1365-3113.1998.00053.x

Melika, G. (2006) *Gall wasps of Ukraine*. Cynipidae. *Vestnik Zoologii*, 21 (Supplement), 1–644.

Melika, G., Tavakoli, M. & Stone, G.N. (2011) A new species of *Andricus* Hartig oak gallwasp from Iran (Hymenoptera: Cynipidae, Cynipini). *North-Western Journal of Zoology*, 7 (2), 286–290.
https://doi.org/10.11646/zootaxa.3760.2.5

Monzen, K. (1953) Revision of the Japanese gall wasps with the descriptions of new genus, subgenus, species and subspecies (I). Cynipidae (Cynipinae), Hymenoptera. *Annual Report of Gakugei Faculty, Iwate University*, 5, 15–21.

Mutun, S., Dinç, S., Bozsó, M. & Melika, G. (2014) Four new species of *Andricus* Hartig oak gallwasp from Turkey (Hymenoptera: Cynipidae, Cynipini). *Zootaxa*, 3760 (2), 241–259.
https://doi.org/10.11646/zootaxa.3760.2.5

Nicholls, J.A., Preuss, S., Hayward, A., Melika, G., Csóka, G., Nieves-Aldrey, J.-L., Askew, R.R., Tavakoli, M., Schönrogge, K. & Stone, G.N. (2010) Concordant phylogeography and cryptic speciation in two Western Palaearctic oak gall parasitoid species complexes. *Molecular Ecology*, 19, 592–609.
https://doi.org/10.1111/j.1365-294X.2009.04499.x

Nicholls, J.A., Melika, G. & Stone, G.N. (2017) Sweet tetra-trophic interactions: multiple evolution of nectar secretion, a defensive extended phenotype in cynipid gallwasps. *American Naturalist*, 189, 67–77.
https://doi.org/10.1086/689399

Nicholls, J.A., Melika, G., DeMartini, J. & Stone, G.N. (2018) New species of *Dryocosmus* Giraud gallwasps from California (Hymenoptera: Cynipidae: Cynipini) galling *Chrysolepis* Hjelmq. (Fagaceae). *Zootaxa*, 4532 (3), 407–433.
https://doi.org/10.11646/zootaxa.4532.3.6

Nicholls, J.A. & Pujade-Villar, J. (2020) Re-instatement of the species name *Callirhytis erythrosoma* (Dettmer, 1933), with comments on other *Callirhytis* species (Hymenoptera: Cynipidae). *Butlletiì de la Institucioì Catalana d'HistòIria Natural*,

84, 31–34.

Pénzes, Z., Tang C.-T., Stone, G.N., Nicholls, J.A., Schwéger, S., Bozsó, M. & Melika, G. (2018) Current status of the oak gallwasp (Hymenoptera: Cynipidae: Cynipini) fauna of the Eastern Palaearctic and Oriental Regions. *Zootaxa*, 4433 (2), 245–289.
https://doi.org/10.11646/zootaxa.4433.2.2.

Pujade-Villar, J., Tavakoli, M., Melika, G. & Ferrer-Suay, M. (2015) *Andricus synophri* (Hymenoptera: Cynipidae), a new species of oak gallwasp from Iran. *Journal of Insect Biodiversity and Systematics*, 1 (1), 1–10.

Pujade-Villar, J., Wang, Y., Tang, G., Shen, J. & Ferrer-Suay, M. (2016) *Andricus mukaigawae* and *A. kashiwaphilus* from China with remarks of morphological differences and inquilines (Hymenoptera: Cynipidae). *Butlletiì de la Institucioì Catalana d'HistoÌria Natural*, 80, 17–24.

Pujade-Villar, J., Wang, Y., Guo, R., Cuesta-Porta, V., Arnedo, M.A. & Melika, G. (2020) Current status of *Andricus mairei* (Kieffer), with synonymization of two species from China (Hymenoptera: Cynipidae). *Zootaxa*, 4808, 507–525.
https://doi.org/10.11646/zootaxa.4808.3.6

Ronquist, F. (1999) Phylogeny, classification and evolution of the Cynipoidea. *Zoologica Scripta*, 28, 139–164.
https://doi.org/10.1046/j.1463-6409.1999.00022.x

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
https://doi.org/10.1093/sysbio/sys029

Ronquist, F., Nieves-Aldrey, J.L., Buffington, M.L., Liu, Z., Liljeblad, J. & Nylander, J.A.A. (2015) Phylogeny, Evolution and Classification of Gall Wasps. The Plot Thickens. *PLoS ONE*, 10 (5), e0123301.
https://doi.org/10.1371/journal.pone.0123301

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

Shinji, O. (1940) On two new species of Cinipidae [sic] (Hymenoptera). *Insect World*, 44, 258–260. [in Japanese]

Tang, C.-T., Melika, G., Yang, M.-M., Nicholls, J.A., Csóka, G. & Stone, G.N. (2009) First record of an *Andricus* oak gallwasp from the Oriental Region: a new species from Taiwan (Hymenoptera: Cynipidae: Cynipini). *Zootaxa*, 2175, 57–65.
https://doi.org/10.11646/zootaxa.2175.1.6

Tang, C.-T., Melika, G., Yang, M.-M., Nicholls, J.A. & Stone, G.N. (2011) New species of oak gallwasps from Taiwan (Hymenoptera: Cynipidae: Cynipini). *Zootaxa*, 2865 (1), 37–52.
https://doi.org/10.11646/zootaxa.2865.1.2

Tang, C.-T., Sinclair, F., Yang, M.-M. & Melika, G. (2012) A new *Andricus* Hartig oak gallwasp species from China (Hymenoptera: Cynipidae: Cynipini). *Journal of Asian-Pacific Entomology*, 15, 601–605.
https://doi.org/10.1016/j.aspen.2012.07.005

Tang, C.-T., Melika, G., Nicholls, J.A., Yang, M.-M. & Stone, G.N. (2020) A new *Cycloneuroterus* Melika & Tang oak gallwasp species (Hymenoptera: Cynipidae: Cynipini) associated with *Lithocarpus* (Fagaceae) from Taiwan. *Proceedings of the Entomological Society of Washington*, 122, 184–196.
https://doi.org/10.4289/0013-8797.122.1.184

Tavakoli, M., Melika, G., Sadeghi, S.E., Pénzes, Z., Assareh, M.A., Atkinson, R., Bechtold, M., Mikó, I., Zargaran, M.R., Aligolizade, D., Barimani, H., Bihari, P., Pirozi, F., Fülöp, D., Somogyi, K., Challis, R., Preuss, S., Nicholls, J.A. & Stone, G.N. (2008) New species of oak gallwaps from Iran (Hymenoptera: Cynipidae: Cynipini). *Zootaxa*, 1699 (1), 1–64.
https://doi.org/10.11646/zootaxa.1699.1.1

Wachi, N. & Abe, Y. (2010) Taxonomic status of the oak gall wasp *Callirhytis hakonensis* (Hymenoptera: Cynipidae), with description of the sexual generation. *Annals of the Entomological Society of America*, 103, 322–326.
https://doi.org/10.1603/AN09128