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Alternation of generations in *Andricus corruptrix* (Schlechtendal): comments on and description of a new sexual form (Hymenoptera: Cynipidae)

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Abstract

Life cycle of *A. corruptrix* (Schlechtendal, 1870) is treated and corrections to previous experiments are discussed. A new sexual form for *A. corruptrix* is herein described, while *A corruptrix* forma *larshemi* is considered a valid species and for taxonomical reasons is renamed as *Andricus improprius* **n. stat & n.sp**, only known by the sexual form, and not linked with *A. corruptrix*. Lectotypes for *A. improprius* n. stat & n. sp. (= *A. larshemi* not available) are also designated.

Contents

Introduction

In most oak gallwasps the reproduction is an example of cyclical parthenogenesis or heterogony. The lifecycle involves alternation of a bisexual generation and a partenogenetic (unisexual or asexual) generation. The two generation are strictly alternating. The cycle is commonly completed within a single year. In some species the two generations ate morphologically different and develop in galls of different types on different parts of the host plant. The link between the unisexual and bisexual generations of one species can be revealed by carefully controlled rearing experiments. In the large genus *Andricus* for instance, in Europe, the two generations of many species are known (Pujade-Villar *et al.*, 2001) but many other species are known only by their unisexual generation and a few other by their bisexual generation only. Modern molecular biology methods, for example DNA sequencing, can help to suspect a specific link between two previously unlinked bisexual and unisexual forms. Rearing experiments remain the necessary method to determine the two alternating generations of a species.

In most species the galls of the two alternating generations develop on the same oak species. In the case of *Andricus kollari* the gall of the unisexual generation develops on *Quercus robur*, *Q. petraea* and *Q. pubescens*. First studies of alternation of generations in the *Andricus kollari* group were made by Beijerinck (1902), who found that *Andricus circulans*, a sexual form galling another oak species, *Quercus cerris*, was the sexual generation of *Andricus kollari*. Such a situation is called heteroecism. These experiments were considered as doubtful by many hymenopterologists of his time, until Marsden-Jones (1953) and Folliot (1964) confirmed their results.

The genus *Andricus* contains several groups of neighbouring oak gallwasps (Stone & Cook, 1998). One of them, called the *kollari* group (Bellido et

al., 2003), contains the species listed in table 1. Docters van Leeuwen (1956) and Docters van Leeuwen & Dekhuijzen-Maasland (1958) studied the lifecycle of two other species of this group, *Andricus lignicolus* and *Andricus corruptrix*. They collected galls of the unisexual form of these two species on *Q. robur* and they described, also on *Q. cerris*, the sexual form of *A. corruptrix* and *A. lignicolus*, respectively named '*larshemi*' and '*vanheurni*'. Wiebes-Rijks (1978) gave diagnostic characters to separate the three known sexual forms (*A. kollari, A. lignicolus* and *A. corruptrix*). These three species, now widespread in a great part of Europe, are not native in The Netherlands and were introduced together with one of their hosts, *Q. cerris*. This introduction enabled species of the *A. kollari* group, once restricted to Eastern Europe, to colonize new zones (Quinlan, 1974; Askew & Neill, 1993).

After Beijerinck and Docters van Leeuwen, the status of the above three heterogonic species was thought to be the following:

Unisexual form	Sexual form
A. kollari (Hartig, 1843)	*circulans* Mayr, 1870
A. lignicolus (Hartig, 1840)	*vanheurni* D. van L. & D.-M., 1958
A. corruptrix (Schlechtendal, 1870)	*larshemi* D. van L. & D.-M., 1958 [not available]

One of us (R. F.) found in Rennes (Brittany, France) similar unisexual galls to those named *A. corruptrix* in Docters van Leeuwen pictures. Experiments with the unisexual adults were undertaken in order to obtain sexual generation and to compare it with the sexual generation obtained by Docters van Leeuwen and other known sexual generations of species of the *kollari* group.

Material and methods

At first, it was observed, in a glass jar that *A. corruptrix* females could lay eggs in *Q. cerris* buds (one egg was found after dissection in the heart of a bud).

Different experiments were made, three of them on *Q. cerris* with one unisexual female each. In one experiment the oak branch died too early after six months. In another nothing was obtained. The third experiment was successful and is described hereunder in more details.

One female of *A. corruptrix* reared in Rennes on the 25th of June, 1997 was taken to Puilboreau (Baillac), near to La Rochelle, a more southern place in France where, despite intense monitoring, *A. corruptrix* has never been found. There, on the 27th of June, 1997, it was placed inside a sleeve on *Quercus cerris*.

Table 1. Alternation of generations in *A. kollari* group

Unisexual form	*Sexual form*	*Sexual form host tree*	*Author closing cycle*
A. kollari	*A. circulans*[1]	*Q. cerris*	Beijerinck (1902)
A. hispanica		*Q. suber*	Pujade-villar (*unpl. data*)
A. lignicolus	*A. vanheurni*[3]	*Q. cerris*	D.v.L & D-M (1958)
A. corruptrix (=*A. ambiguus*[2])		*Q. cerris*	Present paper
A. infectorius	Unknown[4]	*Q. cerris?*	——
A. amblycerus	Unknown	*Q. cerris?*	——
A. aries	Unknown	*Q. cerris?*	——
A. caliciformis	Unknown	*Q. cerris?*	——
Unknown	*A. improprius*[5]	*Q. cerris*	——

(1) According to Pujade-Villar, 1992 and Pujade-Villar *et al.* 2001; known but not described; before mentioned as *A. kollari* in the Iberian Peninsula.

(2) Non valid species according Bellido, Melika & Pujade-Villar (*submitted*).

(3) The new sexual, in this paper, do not have a specific name, following the article 15 of the International Code of Zoological Nomenclature.

(4) *A. burgundus* has been recorded as the sexual generation of *A. infectorius* (=*tinctoriusnostrus*, according to Melika *et al*, 2000), but recent papers argue against that (Stone & Cook, 1998; Cook *et al*, 1999).

(5) **n. stat** and **n. sp.** to *Andricus corruptrix* forma *larshemi* (in this paper).

The sleeve was left from 27th June, 1997 until 20th April, 1998, to avoid oviposition by *A. kollari* and *A. lignicolus* (although this last species is very rare in the zone) and later, predation by birds, which frequently attack growing galls in the oak buds. We obtained galls and insects of the sexual generation which will be treated further in more details.

Our specimens were compared with both unisexual and sexual material obtained by Docters van Leeuwen and Dekhuijzen-Maasland in their experiments, deposited in Zoölogisch Museum Amsterdam (Netherlands). Unfortunately, only 4 unisexual females of *Andricus corruptrix* and 2 sexual females of *A. larshemi* are left of the material used in the experiments of Docters van Leeuwen. Our specimens were also compared with material of the unisexual and sexual froms of *A. lignicolus* and *A. kollari*, experimentally obtained by Roger Folliot. Unfortunately no types of *A. vanheurni* were found among the Docters van Leeuwen material collections. Only 3 unisexual females of *A. lignicolus* used in the experiments were left (Hogenes, *pers. com.*).

SEM pictures were made by the second author. The pictures were made at low voltage and without coating to preserve specimens from damage.

We follow the current terminology of morphological structures as given in Gibson (1985), Ronquist and Nordlander (1989), and Fergusson (1995). Abbreviations for fore wing venation follow Ronquist and Nordlander (1989). The measurements and abbreviations used herein include: F1 – F12, 1st and subsequent flagellomeres; POD (postocellar distance), the distance between the inner margins of the posterior ocelli; OOD (oculo-ocellar distance) for distance between inner margin of eye and lateral ocelli; COD (central-ocellar distance) for distance between lateral and central ocelli.

Results

In April, 1998, 8 isolated galls were found inside the sleeve, from which we reared 5 alive females, 2 males and one dead parasitoid. This parasitoid is not a cynipid parasitoid, and may come from the branch used in the experiment. One gall remained closed.

The bisexual form of Andricus corruptrix *(Schlechtendal)*

Sexual adults obtained from the experiment were compared with *A. larshemi* types from Docters van Leeuwen collection, sexual adults of *A. kollari (=circulans)* and *A. lignicolus (=vanheurni)* experimentally obtained by Folliot and descriptions present in the literature (Wiebes-Rijks, 1978). They are clearly different from all these forms.

We compared also unisexual females used by Docters van Leeuwen in his experiments with our *A. corruptrix* female and we found they belonged to the same species. As the unisexual females appear to be identical and the obtained sexual forms different, one of the two experiments must have been contaminated by another species. Docters van Leeuwen & Dekhuijzen-Maasland were successful in their attempt to produce unisexual form galls from sexual insects but in other experiments, they obtained sexual galls under arguable conditions since nets were kept on the host for only two weeks (Docters van Leeuwen & Dekhuijzen-Maasland, 1958). In our opinion the contaminant could not be *A. lignicolus* or *A. kollari* since their sexual generations are different, but an undetected species of the *A. kollari* group which has been confused with other species. Consequently, the name *A. larshemi* points to a valid species the unisexual generation of which is unknown.

To sum up, the sexual form of *A. corruptrix* is not the form *larshemi* described by Docters van Leeuwen but a new form, which we describe hereunder.

Andricus corruptrix *(Trotter) new bisexual form*

Studied material: Experimental material, 2 males and 5 females of the previously described experiment (VI-1997/ IV-1998); 2 males and 2 females; material deposited in Barcelona University; 2 females (also paratypes) deposited in MNHN (Paris).

Length: 1.6-1.8 mm (for males) and 1.8-2 mm (for females).

Colour: All the body black. Wing veins dark brown.

Female head (Figs. 1a & 1b). Without pubescence; in dorsal view around 2.5 times wider than long. Genae coriaceous, not broadened behind compound

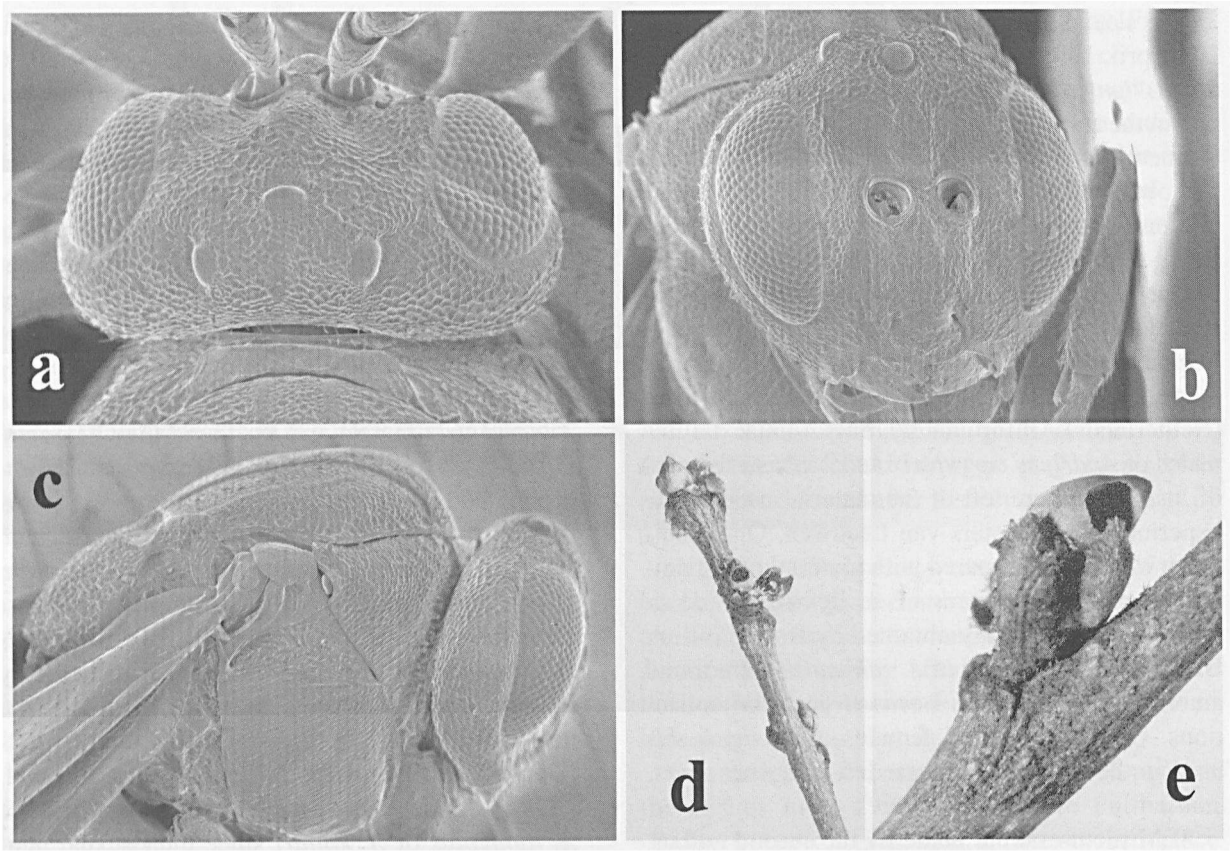

Fig. 1. A. corruptrix bisexual form: a) head of in dorsal view; b) head in frontal view; c) lateral view; d) branch with some galls; e) isolated gall.

eyes. POD twice OOD; OOD 1.5 times lateral ocellus diameter and more or less equal to COD (ratio POD:OOD:COD:lateral ocellus diameter is 45:23:23:15). Coriaceous sculpture. Clypeus conspicuous and suboval in shape. Face with only some very short and weak irradiating striae around clypeus, never reaching neither antennal toruli nor compound eye margin. Transfacial line more or less equal to eye height. Diameter of toruli around twice the distance between them and slightly larger than distance between toruli and eye margin. Male head similar to female.

Female antenna (fig. 2a) with 13 segments, 0.8 times body length or slightly longer; pedicel 2 times longer than wide; F1 is 1.2 times longer than F2 and 1.6 times pedicel length; following flagellomeres gradually decreasing in length, last flagellomeres conspicuously longer than wide and last more or less twice its width. Male antenna (fig. 2b) with 14 segments, the third one curved, dorsally flattened, proximally excavate and distally expanded; number of sensilla in each segments higher (6-8) than in females.

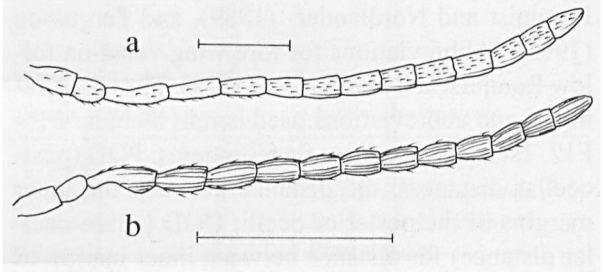

Fig. 2. Antenna of *A. corruptrix* bisexual form: a) female (scale bar 200 micrometres); b) male (scale bar 500 micrometres)

Female mesosoma (figs. 3b, 3d, 3f). Without pubescence except for some hairy zones in the propodeum, with coriaceous sculpture. Notauli com-

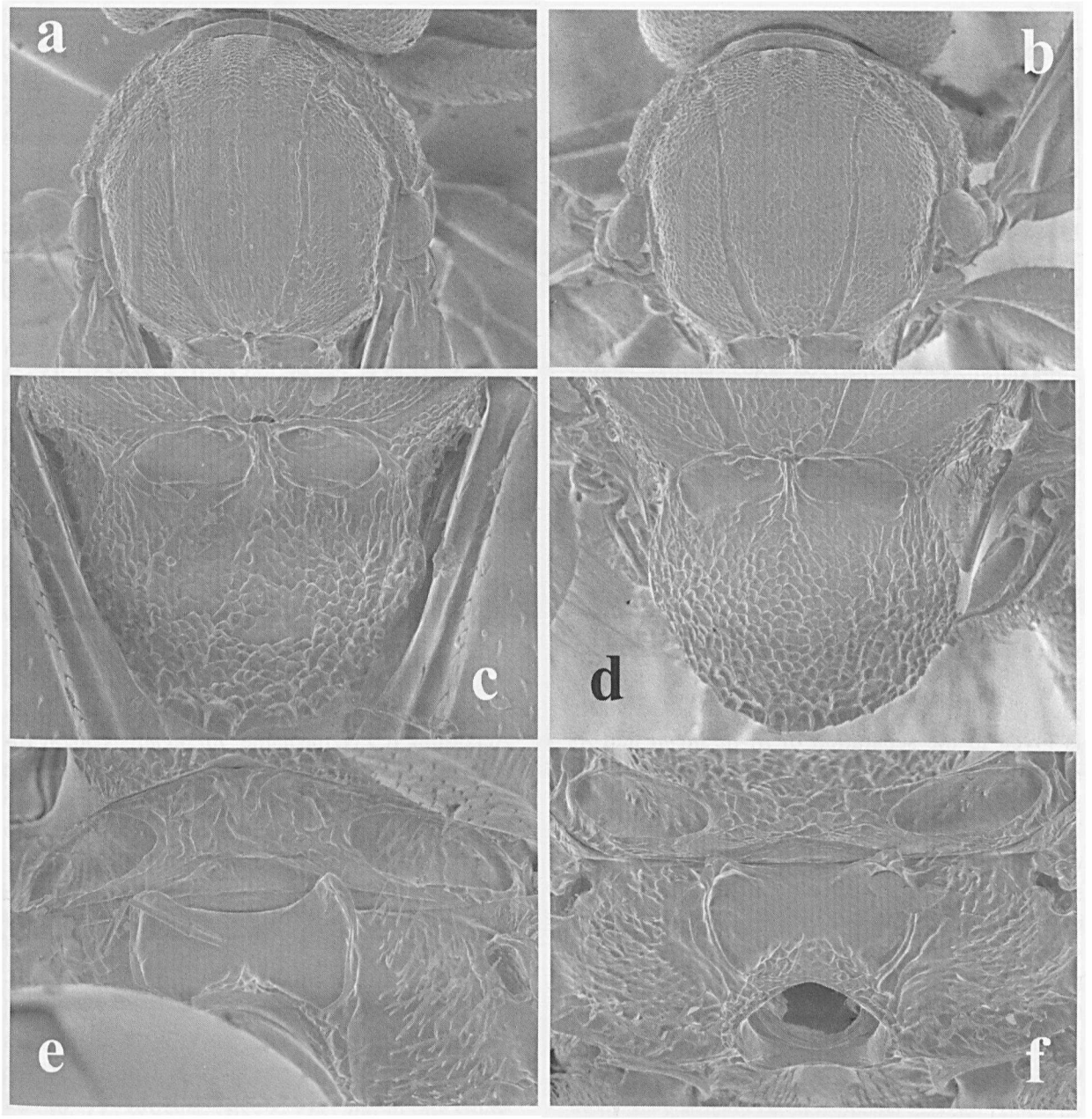

Fig 3. Scutum in dorsal view (a, b), scutellum in dorsal view (c, d) and propodeum (e,f) of the bisexual form of *Andricus improprius* new status & n. sp. (a, c, e) and *A. corruptrix* new form (b, d, f)

plete and deep in all its length, always reaching pronotal margin, converging posteriorly and widening (posterior notauli width at least one third of distance between them), delimiting an area with regular closely reticulate sculpture (not longitudinally striated) (Fig. 3b). Median mesoscutal impression absent. Mesopleuron (Fig. 1c) almost completely striated with some striation also in pronotum. Scutellum subquadrate, only slightly wider than long, with closely reticulated sculpture, not marginated laterally and not lobed posteriorly. Scutellar foveae (Fig. 3d) oval, with a transversal disposition, smooth, shiny and not pubescent inside, not delimited posteriorly by a carina and separated from each other by

a median carina. Lateral carinae of propodeum (Fig. 3f) thin, of an uniform thickness, bowed outwards, internal area shiny and smooth, not closed in its superior part (a carina close to the superior part of propodeal area in *A. larshemi*). Wings hyaline. Forewing margin with short and scattered setae in its anterior margin; radial cell 4-4.5 times longer than broad; 2r vein angled; areolet usually conspicuous. Tarsal claws of legs with an acute basal lobe and forming a close angle; anterior tibiae provided with short and applied hairs. Male mesòsoma similar to female.

Female metasoma. Slightly shorter than head plus mesosoma together; without pubescence except at the basis of the 3rd abdominal tergite. Third abdominal tergite covering between ½ and ¾ of metasoma in dorsal vision. Ventral spine of hypopigium slightly longer than broad, with sparse setae, which do not form an apical tuft. Male metasoma smaller than mesosoma.

Diagnosis. It can be easily separated from other sexual forms of the *A. kollari* group by the following combinations of characters (special emphasis is given to the separation of *A. larshemi* and *A. corruptrix* bisexual form because they are the most similar forms). Upper part of propodeum not closed by a complete carina, while in *A. larshemi* it is conspicuously closed (figs. 3e & 3f), mesoscutal sculpture between notauli regularly reticulated, not elongated like in *A. larshemi* (figs. 3c & 3d) and scutellar foveae not delimited posteriorly while they are delimited in *A. larshemi* (figs. 3c & 3d), sculpture between notauli regularly reticulated (like in *A. circulans*) but never elongated like in *A. larshemi* (figs. 3a & 3b), scutellar sculpture weaker than in *A. lignicolus* (= *vanheurni*) or *A. kollari* (= *circulans*), and regularly reticulated and not coarse.

Distribution. Only known in experimental conditions from France, where the unisexual form has probably been introduced recently.

Gall. Similar to other sexual galls of the *A. kollari* group. A small bud gall (fig. 1d), measuring between 2 and 2.5 mm from basis to top, on *Q. cerris*, isolated (unlike those of *A. circulans* or *A. larshemi*), with its basal part hidden from view by bud-scales and apical part projected outside. The surface of the gall is brown, nearly smooth, without striation, and with a short and deciduous pubescence. The tops are pointed, not rounded, and the gall wall is very thin. Adults leave the gall through a circular, big and lateral opening below the top.

Taxonomic comments on Andricus corruptrix f. larshemi *D. van L. & D.-M., 1958*

The insects named "*larshemi*" by Docters van Leeuwen & Dekhuijzen-Maaland (1958) do not represent the sexual form of *A. corruptrix* but correspond to another valid species only known by its sexual form. Consequently, what is the status of the name "*larshemi*"?.

As evidences in this study show the life cycle of *Andricus corruptrix* was erroneously described by Docters van Leeuwen (1956: 255). The sexual form was given the name *A. corruptrix* forma *larshemi* in Docters van Leeuwen & Dekhuijzen-Maasland (1958: 102, 104) and not in Docters van Leeuwen (1956) as it's stated in Wiebes-Rijks (1978: 140). According ICZN, the name "*larshemi*" is not available for two reasons: because it's described as a form of a previous species (art. 45.6.1) and because it's described from galls and not adults (arts.1.3.6 i 13.1.1).

Actually, Docters van Leeuwen & Dekhuijzen-Maasland (1958: 102) stated that sexual adults of "*larshemi*" form are indistinguishable from bisexual adults of *Andricus kollari*. Moreover Eady & Quinlan (1963: 49) gave differences between sexual females of "*larshemi*" and "*circulans*", since males were unknown to them (Eady & Quinlan, 1963: 52). These authors never explicitly mentioned that "*larshemi*" belong to a taxonomical category other than 'form', and thus the name continues as not available. Later, Wiebes-Rijks (1978) gave diagnostic characters for both sexes of "*larshemi*" but continued considering them as a form of *A. corruptrix*, and thus the name can't be used according ICZN (art. 15.2, 45.6.1 i 46.6.3).

First author giving "*larshemi*" a different taxonomic status (*A. corruptrix* ssp *larshemi*) was Ambrus (1974: 26), but his name can't be used either, because he only described galls, and according ICZN

again, infra specifics terms can't be used after 1960 (art. 15.2) and gall descriptions are not considered valid for taxonomic purposes after 1930 (art. 1.3.6). Therefore "*larshemi*" remains not available after Ambrus' paper.

Finally, Melika *et al.* (2000: 269) consider "*larshemi*" as a different species from data shown in this study, but it's not characterised morphologically, and thus "*larshemi*" can't be available either (art. 1.3.6).

At last we consider the previously named form "*larshemi*", neither linked to *Andricus corruptrix* nor to *Andricus kollari* and *Andricus lignicolus* as a valid species only known by its sexual form but for taxonomic reasons we rename this species as *Andricus impropius* **n. stat. & n. sp.**

Andricus improprius *Bellido & Pujade-Villar n. stat. & n. sp.*

Andricus corruptrix forma *larshemi* Docters van Leeuwen & Dekhuijzen-Maasland (1958) [not available]
Andricus corruptrix (=*larshemi*) Eady & Quinlan (1963) [not available]
Andricus corruptrix forma *larshemi* Wiebes-Rijks (1978) [not available]
Andricus corruptrix ssp *larshemi* Ambrus (1974) [not available]
Andricus larshemi Melika, Csóka & Pujade-Villar (2000) [not available]

Studied material (deposited in Zoölogisch Museum Amsterdam). Lectotype ♀ herein designated with following labels: "*Andricus corruptrix* Schlechtendal forma larshemi ♂♀ D. v. L. et J. M.D.-M. Leersum, 10.v.1955" (handwriting); "Lectotype" (red label); "*Andricus improprius*, Bellido & Pujade-Villar det. 2000" (white label). Paralectotype ♀ with the same labels except for a "Paralectotype" label (red).

Diagnostic characters for adults of *A. improprius* are given in Wiebes-Rijks (1978) and in this study (fig. 3a, c, e), galls are described in Docters van Leeuwen & Dekhuijzen-Maasland (1958).

Discussion

The time of sleeve enclosure in our experiment was long: almost ten months from June to following April. The enclosure was, at first, intended to prevent contamination by *A. kollari* and *A. lignicolus*. This last species can emerge as early as May in Brittany but is very rare in Baillac (France) where since several decades it has been found only once. *A. kollari*, in Baillac emerges (in the 2nd year) usually from July. At any rate, the sexual adults obtained do not belong neither to *A. lignicolus (=vanheurni)* nor to *A. kollari (=circulans)*, as we have discussed above.

The presence of both sexes originating from one unisexual female may seem strange as the norm in *Andricus* is usually to find sexual adults originating from one unisexual female of only one sex (all males or all females). But in the allied species *A. kollari*, Folliot (1964: 493) observed a similar situation in several instances, usually one or a few sexual females in the progeny of a male producing unisexual female and eventually when small numbers are concerned, more females than males. At any rate both sexes described here are morphologically similar and different from the other three known sexual forms in the group. Therefore we consider the new sexual form as the valid form alternant with *Andricus corruptrix* (Trotter).

To sum up, all the known life-cycles of the species of *A. kollari* group are presented in table 1. Sexual generation of other species of the group may have *Q. cerris* as host as most known species but, the host tree of these sexual generations is still unknown and therefor here indicated with a question mark.

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