

**Female ectodermal genitalia of the taxa of the *Kelisia guttula* - group (Homoptera Fulgoromorpha Delphacidae): not only an example for specialized coorganization with male genitalia without obvious reasons, but also a character set apt for species discrimination in westpalaeartic taxa?**

**REINHARD REMANE & ADALGISA GUGLIELMINO**

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**Abstract:** In the course of evolution male and female external and internal ectodermal genitalic structures in the taxa of the monophyletic *Kelisia guttula*-group have been enlarged and differentiated in a very special way in comparison to plesiomorphic taxa of Kelisiinae. Functional reasons for this "orthogenetic" evolution are not yet known, as it seems. In evolutionary "coorganization" the evolution of a proportionally very large genitalic segment and an extremely long, thin and flexible aedeagus in the males is "answered" (for there seem to be - other than in some other insect taxa, e. i. Diptera Tephritidae - no special "female" functions like oviposition or "sperm handling" which may act as "selective forces" on these structures, by this changing their morphology) by the females with the development of a special duct of approximately "edeagal length" guiding and keeping the male aedeagus during copulation. This "edeagal duct", which morphologically is "folded off" from the genital room, starts at the dorsal base of the female's genital room and ends opposite the depart of the oviductus communis (leading to the spermatheca as well as to the ovaries). It is much longer than the genital room, but it remains connected with it by a thin ligament. It is provided with a variety of sclerotized structures. This could be interpreted as a "lock and key" mechanism to prevent successful mating between specimens belonging to different species, but such matings are prohibited already by species-specific vibratory signals acting as "pre-mating isolating mechanism". As in the *K. guttula*-group there exist several species-groups containing externally very similar species, in which the females could not be identified down to species up to now (resulting in "handicaps" for biogeographical and ecological analyses), we examined these structures looking for species-specific characters enabling the safe identification not only of males, but of females, too. As a result all females of this group now may be safely identified due to such species-specific characters present in their internal ectodermal genitalia. The populations of "*Kelisia irregulata* Haupt" from Spain and western France have shown to be that different from the allopatrically distributed central european populations, that they seem to be a genpool of their own. So we decided to describe these populations as a species of its own: *Kelisia occirrega* n. sp. (Type locality: Spain, Prov. Pamplona, Isaba in the Valle del Roncal in the southwestern Pyrenees). This taxon ought to keep its species rank unless intermediate, transitional specimens will be discovered in the "gap" between the two taxa (situated in eastern France) indicating the existence of a "hybrid belt".

As known, one of the aims of taxonomic research is to detect character states, which enable a researcher safely to decide to which of two or more otherwise very similar species a certain specimen belongs. Most favourable are those character states, which may be easily seen and persist even if the specimen is dead and conserved by appropriate techniques.

Unfortunately, in many groups of animals this aim has not yet been achieved: one of the sexes and/or juvenile specimens have to remain unidentified.

This situation exists also in the "guttula-group" of the planthopper genus *Kelisia* Fieber. The number of species recognized in this species-group has not only increased during the past years, but the characters used for species recognition and discrimination have changed, too: while in former times (RIBAUT 1934; WAGNER 1939) it was possible to recognize the alleged "species" not only by characters of the male genitalia but also by external characters like size, shape, proportions, colour and markings, more recently species have been established or described (REMANE & JUNG 1995, GUGLIELMINO & REMANE 2002) which could be discriminated from their nearest relatives no longer by external characters but by the structure of the male genitalia only. In most of these cases their females had to remain unidentified.

As such a situation is unfavourable for ecological as well as for biogeographical research, we started an examination of the internal ectodermal parts of the female genitalia in order to find out, whether there might exist species-specific characters or not.

In the monophyletic "*Kelisia guttula*-group" (consisting up to now of 10-11 species: 3 in the eastern part of the Palaearctic Region only: *xiphura* Vilbaste, *bispinifera* Dlabola and *asahinai* Hori, and 8 confined to or reaching into the western Palaearctic: *guttula* Germar sensu Wagner, *sima* Ribaut, *italica* Guglielmino & Remane, *irregulata* Haupt, *vittipennis* J. Sahlberg, *haupti* Wagner, *halpina* Remane & Jung, *hagemini* Remane & Jung) the internal female genitalia are very specially constructed<sup>1</sup>. Directly at the dorsocephal side of the genital-opening following the "Atrium-Platte" there is developed a special duct accompanying the basal part of the "Genitalraum", i. e. the part extending between the cephalodorsal basis of the GVIII and the origin of the duct leading to the ovaries and the receptaculum seminis. This special duct "directs" and "keeps" the male aedeagus during copulation. To succeed in this, it is provided with more or less extended sclerotized walls: some of these sclerotizations are located on its dorsal side, and one at the "end" directly before this duct enters again the genital room. The male of the taxa of the *K. guttula*-group possess not only an absolutely and relatively to the size of the body very enlarged genital segment but also a thin, flexible and extremely elongated aedeagus (see amongst others WAGNER 1963 and ASCHE 1985), which at rest lies curved in a semicircle in the distal half of the male abdomen. "Coorganized" with the length of the aedeagus, the duct in the female genitalia (but not the corresponding part of the genital room!) is considerably elongated and by this is forced to "depart" from the genital room, forming in some taxa a large, undulated, asymmetrically situated lobe. This lobe always stays connected over its complete length with the genital room by a thin, membranous ligament. By this a kind of separation

<sup>1</sup> The non-westpalaearctic taxa *K. xiphura* Vilbaste, *K. bispinifera* Dlabola and *K. asahinai* Hori, 1982 have not yet been investigated due to the lack of material. The description of *K. asahinai* Hori unfortunately lacks important details of the structure of the male genitalia (only tip of the aedeagus shown, subanal appendages neither figured nor described) which render the placement of this species somewhat doubtful.

between "copulation duct" and "oviduct" results, which reminds the ditrysic constructions found in other taxa (e.g. Stenocraninae). This character complex - thin, long and curved aedeagus and detached special "edeagal duct" in the females - is a special feature of the taxa of the "*K. guttula*-group" not present in any other palaeartic or nearctic groups of Kelisiinae. It may be considered as a special synapomorphy "proving" the monophyly of this group of taxa<sup>2</sup>.

To observe the aforementioned characters, it is necessary to macerate the female abdomen in K(OH)/potassium hydroxid (ca. 10%) and after that using a binocular microscope to wash and dissect it in water. After that it may be transferred either as usual into glycerol for detailed observations or (if parts like genital room, oviduct, and bursa copulatrix are to be kept inflated) in water to which formaldehyd has been added (ca. 1:15, see Asche 1985: 27). To examine the details, a magnification of ca. 100x is recommended.

The results of our investigations have to be considered preliminary, for from many species we have examined a rather small number of specimens only: the range of variation of these characters within a population as well as within the geographical range of each taxon thus might be larger than shown here and than known up to now. Nevertheless, the results obtained so far seemed that promising with respect to the aim of species discrimination in this *K. guttula*-group, that we decided to publish them already now: so these our results presented here may be corroborated, or corrected by other homopterologist.

The characters, in which we think to have found differences between the species of this group mainly are:

1<sup>st</sup> The absolute and relative length of the edeagal duct. This length apparently (and as expected) is  $\pm$  correlated with the length of the aedeagus. But exact measuring is difficult (and time-consuming), as this duct is bent and twisted in all directions especially in those taxa, in which it is very long. In addition the way in which this duct is bent differs between specimens of the same species (even if these specimens were caught at the same data in the same place). Nevertheless - as shown by the figures - there is a very short duct in *K. hagemini* Remane & Jung (Fig. 1), this duct is distinctly longer in *K. haupti* Wagner (Fig. 2) and much longer in *K. halpina* Remane & Jung (Fig. 3). These three species were separated in 1995 only (REMANE & JUNG) by morphometric examination of their male genitalia, they are very similar in size, proportions and markings and at that time their females could not be reliably separated. Also in the subgroup of externally very similar species which consists of *K. guttula* (Germar) sensu Wagner, *K. sima* Ribaut and *K. italica* Guglielmino & Remane, at least *K. guttula* (Germar) sensu Wagner (Fig. 4) has a shorter duct than *K. sima* Ribaut (Fig.

<sup>2</sup> This "coorganized enlargement" may be interpreted as being a case of "orthogenetic evolution". Up to now we have not been able to find any external "selection factors" favouring such a "hypertrophic" evolutionary specialisation. But at least - different from the situation found in some other insect groups, e. g. Diptera Tephritidae - selection pressures implied by special "female" functions (e. g. oviposition, "sperm handling") hardly would have changed this special "edeagal duct", which apparently is used for copulation only: an event which takes place hardly more than once in the life of the a *Kelisia* female. For these reasons structures found in the females might have adapted to the evolatory change in the male's genital organs and not vice versa. An explanation as a "lock and key mechanism" in order to prevent mating between specimens belonging to different species seems doubtful, as such mating in Kelisiinae is prevented by species-specific vibratory signals forming a "pre mating isolating mechanism".

5) and especially than *K. italica* Guglielmino & Remane (Fig 6). *K. vittipennis* J. Sahlberg (Fig. 7) and *K. irregulata* Haupt (Fig. 8) have very long ducts, too. The width of the duct in nearly all taxa decreases continuously from the basal part towards its end.

2<sup>nd</sup> The intensity and distribution of sclerotisation of the edeagal duct. This sclerotisation is developed "postmetabolic" (like the apodemes of the tymbal e. g. in Cicadellidae) - it is complete only in fully mature, "old" females. (Whether staining of these structures, e. g. with chlorazol, might render these sclerotized areas visible already in "young" females, should be examined in future). The sclerotisations of the walls are to be found in different parts of the duct - in the basal half the placement and their shape seem to be species-specific (see figures and below). The sclerotisation of the wall at the end of the edeagal duct at the place of its reentrance into the genital room (always separated from the basal sclerotized regions by a non-sclerotized part of the edeagal duct) is always present, but rather small in all taxa except in those females externally looking like *K. irregulata* Haupt, and in *K. halpina* Remane & Jung of the *K. haupti*-subgroup. Its shape varies very much depending on the position from which it is viewed; morphologically it somewhat resembles a more or less curved half or three-quarters tube with irregular margins. To describe it precisely it has to be cut out of the duct - a procedure we did not practise. Its "taxonomical value" might increase by that in future.

3<sup>rd</sup> All taxa of the *K. guttula*-group we have seen possess an "Atrium-Platte", i. e. a sclerotized part of the intersegmental membrane situated cephalad of the GVIII-basis at the entrance into the genital room. The size and the shape of this part seems rather similar to us in those examined taxa which are very similar to each other, but a more detailed investigation of these might show some of them to possess species-specific characters: in *K. halpina* Remane & Jung the dorsal sclerotisation of the edeagal duct arises out of the dorsal center of the "Atrium-Platte", in all other taxa it does not.

How far may be characterized the species of the *K. guttula*-group by features of their ectodermal internal genitalia?

1. *K. guttula* (Germar, 1818) sensu Wagner is one of the most widely distributed species of this group, even if doubtful old records are omitted and even some recent records need to be verified after the separation of *K. sima* Ribaut. We have examined females from western Greece (Korfu), central Italy (Abruzzo), northeastern Austria (Burgenland) and western Germany. Specimens examined so far had an edeagal duct of moderate length (Fig. 4) with a sclerotized part caudad of the end of the Gm IX-stalk. Its part between "Atrium-Platte" and Gm IX-stalk is not sclerotized. The sclerotisation at the end is rather small and in dorsal aspect hidden below the duct's basal part. Variation was found in the way of bends shown by the duct and (age-dependent) the intensity of its sclerotisation. Whether - due to the wide area inhabited by this taxon - there might exist geographical variation or even additional species so far not recognized has to be shown by future research.

2. *K. sima* Ribaut, 1934 is a taxon, whose area of distribution is european and up to now "included" in the area of *K. guttula* (Germar) sensu Wagner (see REMANE & JUNG 1995). In some places, where it was sufficiently abundant, it was found to inhabit a host plant species (*Carex flava* L.) different from that of *K. guttula* (Germar) sensu Wagner (*Carex flacca* Schreber). Its edeagal duct (Fig. 5) is very long and therefore bent back cephalad until the G VIII-rami. Its sclerotisation is either limited to a region caudad of the Gm IX-stalk (Fig. 5), leaving the basal part unsclerotized, or a pair of laterally

situated sclerotized bends reaches cephalad nearly to the end of the "Atrium-Platte" (Fig. 5). The sclerotisation at the duct's end is rather small (like in *K. guttula* (Germar) sensu Wagner). Examined were up to now specimens from Germany (Hesse and Bavaria).

3. *K. italica* Guglielmino & Remane, 2002 very recently described from three localities in the Appennine Mountains of central Italy, might be an endemism of that peninsula. Its edeagal duct is very long and several times distorted (Fig. 6). Its part situated caudad of the Gm IX-stalk is laterally enlarged and heavily sclerotized - a configuration up to now not found in any of the other species. The sclerotisation at the duct's end is rather small and inconspicuous.

As it seems, the females of these three species - very similar in external characters and markings (e.g. big black spot on the genae!) - may be safely distinguished by the structure of their female ectodermal genitalia.

The taxa *K. haupti* Ribaut, *K. halpina* Remane & Jung, and *K. hagemini* Remane & Jung constitute a subgroup of their own: very small, short-legged, more pronounced brachyptery (hind wings of brachypterous specimens  $\pm$  vestigial), their dark markings are similar to those of *K. vittipennis* J. Sahlberg ( $\pm$  continuous dark sublateral vittae, i. e. also pronotum between eyes and scutum brown). The female genitalia, too, are similar to each other but different from those of all other taxa: the bends of edeagal duct are - irrespective of the duct's length - situated vertically, i. e. dorsoventrally (and not laterally as in the other taxa) (Figs. 1-3). The three taxa differ clearly in length and sclerotisation of the edeagal duct:

4. *K. hagemini* Remane & Jung, 1995 has a very short edeagal duct (apparently corresponding to the short aedeagus of the male), which is lightly sclerotized dorsally in its basal part (but this sclerotisation is not in contact with the "Atrium-Platte"), its distal part is very short and hardly bent, its sclerotisation at the duct's end is small and  $\pm$  inconspicuous (Fig. 1). We so far have examined females from Croatia, northern Italy (region of the type locality), and southern Switzerland (Ticino) - whether there exists "geographic variation" has to be investigated later.

5. *K. haupti* Wagner, 1939 has an edeagal duct which is distinctly longer than that of *K. hagemini* Remane & Jung, its sclerotisation is situated in its distal half basally of the narrow bend leading to its distal part (Fig. 2). This distal part is distinctly longer than that of *K. hagemini* Remane & Jung (but much shorter than that of *K. halpina* Remane & Jung), its is bent into an incomplete "oval circle". Its sclerotisation at the duct's end is small like in *K. hagemini* Remane & Jung. Up to now we examined specimens from the northeastern part of its area (which includes the type locality).

6. *K. halpina* Remane & Jung, 1995 has an edeagal duct much longer than that of *K. haupti* Wagner, it is distinctly sclerotized in its basal part - this sclerotisation emerges from the "Atrium-Platte" (an unique configuration) (Fig. 3). The duct's distal part is very long and bent into more than a complete circle. Its sclerotisation at the duct's end is long and curved. Up to now we examined specimens from the type locality in Austria and from southern Switzerland.

Due to these results a safe discrimination of the females of these three taxa may be made, even non-mature females may be identified due to the considerable differences in length and shape of the edeagal duct.

7. *K. vittipennis* J. Sahlberg, 1868 is, like *K. guttula* (Germar) sensu Wagner, according to published records, another taxon with almost transpalaeartic distribution - thus at least geographical variation might exist. Other than *K. guttula* (Germar) sensu Wagner it

is absent from regions with Mediterranean climate: there it is restricted to mountain regions of the north<sup>3</sup>. We have examined up to now specimens from northern, northwestern and central Germany, and from northern Italy (Alpi Bergamasche). In these specimens the edeagal duct is rather long (Fig. 7), though shorter than in *K. sima* Ribaut, *K. italica* Guglielmino & Remane and *K. irregulata* Haupt. In the German specimens its basal part (up to the first lateral bend) is rather long, bending of the distal part  $\pm$  simple (Fig. 7), in the Italian specimens this basal part is shorter, the part distal of it more twisted, its bends reach more cephalad. Simply spoken, the edeagal duct has no special features and looks somewhat intermediate between that of *K. guttula* (Germar) sensu Wagner and that of *K. sima* Ribaut. The sclerotisation at the duct's end is small and inconspicuous like in these taxa, too. So in this case the recognition of females by structures of their genitalia alone seems difficult. But the differences in the size of the black markings (black spot on genae less extended to the head's basis, on the contrary black streak on pronotum connecting dark or red eyes with dark lateral parts of scutum in *K. vittipennis*) clearly separate *K. vittipennis* from *K. guttula* (Germar) sensu Wagner and *K. sima* Ribaut.

8. *K. irregulata* Haupt, 1935. This species is "reliably" recorded from Europe only: described from Germany (south of the northern Plains, type locality Blaubeuren, situated in Baden-Württemberg west of Ulm) it was recorded by NAST (1972, 1987) in addition from Austria, Slovakia and France (the latter apparently is based on a publication of RIBAUT (1959: 397) who recorded it from eastern France near the Swiss border: Dépt. Ain. Recently it was recorded from northwestern France, e. g. Dépt. Eure, northwest Paris, REMANE & DELLA GIUSTINA, 1991). In addition the first author (Remane) has collected it in Switzerland, in the eastern Iberian Peninsula (Spain) in an area from the Sierra de Segura in the south, the Sierra de Guadarrama in the west and in the Cordillera Cantabrica in the north-west up to the Eastern Pyrenees as well as in the French Roussillon (Dépt. Aude).

No clear differences concerning size, proportions, degree of wing polymorphism, colour and markings were discovered between the specimens of those widely separated localities. They all show a spot on their genae which reaches just the anterior part of the basal field and their dark sublateral longitudinal streak is clearly interrupted on the pronotum like in *K. guttula* (Germar) sensu Wagner, *K. sima* Ribaut and *K. italica* Guglielmino & Remane (and some taxa of other species groups). But an examination of the internal ectodermal parts of the female genitalia revealed the existence of two clearly separable morphotypes which seem to be geographically separated: 1) all females from central and western Germany and from the Alps bear a very characteristic bifid sclerotisation in the dorsal wall of the edeagal duct near its base (Fig. 8). - 2) all females from the Iberian Peninsula and from western France (Dépt. Eure) so far examined lack such a sclerotized structure at that place (see Fig. 9a).

Both population groups have in common a very long edeagal duct, in coorganization with the long male aedeagus, and a rather long sclerotisation at the duct's end compared with those parts in *K. guttula* (Germar) sensu Wagner and especially *K. vittipennis* J. Sahlberg. The males, too, are separable in two corresponding groups by the length of the subanal appendages: These appendages are rather short in the central European

<sup>3</sup> NAST (1972) mentions "Algeria", but this is based according to METCALF (1943) on a record by FOKKER (1900) only, who published a list of species he received (bought?) from Schmiedeknecht, who pretended that he had collected them in Algeria. In fact these *K. vittipennis*, if the identification should prove to be correct, very probably were collected in Central Germany...

populations (reaching caudad only about half the length of the anal tube, their tips are situated - in resting position - at the base of the anal area, in some specimens not even reaching this base). They are distinctly longer in the populations of western France and the Iberian Peninsula (reaching caudad at least till three quarter or four fifth of the anal tube's length, their tips are at the distal end of the weakly chitinized area around the anus on the dorsal side of the anal tube).

Thus at moment we are able to distinguish two allopatrically distributed "morphotaxa". The "western" taxon needs to be described. We have decided to give it species rank, but if further research might bring to light the existence of a "transitional zone" with morphologically  $\pm$  intermediate specimens indicating hybridisation under natural circumstances between the two morphotaxa, then the western taxon would need to be reduced to subspecific rank.

Such a "hybrid belt", if it exists, should be situated in the east of France. Unfortunately we have not seen any specimens from this region (and - except the Ain record of Ribaut, 1959 - there seem to exist no records).

*Kelisia occirrega* n. sp. (Figs 9a, 9b)

In general appearance, dimensions, proportions, degree of brachyptery, colour and markings of body, legs, and fore wings not significantly different from *K. irregulata* Haupt.

Male genitalia very similar to those of *K. irregulata* Haupt, but subanal appendages (Fig. 9b) longer, reaching caudad at least till three quarters of the anal tube's length (their tips are situated at the distal end of the weakly chitinized anal area).

Female genitalia similar to those of *K. irregulata* Haupt too, but lacking the conspicuous, bifid sclerotisation in the base of the dorsal wall of the very long edeagal duct (Fig. 9a).

Distribution: So far known from Iberian peninsula (in a region at the moment limited by Sierra de Segura - Sierra de Cazorla in the south, Sierra de Guadarrama in the west, and the Cantabrian Mountain Range east of Picos de Europa in the northwest) and from western France (Dépt. Aude, Seine-et-Marne, Eure). Its area's western border on the Iberian Peninsula and especially (north-) eastern in France need to be clarified by additional research. Inside the limits shown here, *K. occirrega* n. sp. was found in the Montes Universales, on and around the Sierra de Albarracin, the Sierra de Gudar and its surrounding, the southwestern Pyrenees (Valle Roncal) and the southeastern Pyrenees (Sierra del Cadi).

Ecology: Like *K. irregulata* Haupt found especially on calcareous soils (open, dry, and sunny as well as rather moist). Host plants are apparently *Carex* spp. The French localities are situated at rather low altitude (below 300m except the one in the Corbières), the Iberian in montaneous sites between 1000 and 1800m altitude.

Specimens examined: Holotypus 1M brachypt.: Spain, Prov. Pamplona, Valle del Roncal: north of Isaba, ca. 950m, 22.09.1973, leg. R. Remane in coll. Remane, FB Biologie Philipps-Universität Marburg. Paratypes (all leg. Remane): 1F same locality and data as Holotype. Spain: Cordillera Cantabrica, south infra Piedras Luengas (Prov. Palencia), 15.08.1978, 1M; east infra Puerto San Glorio (Prov. Santander), ca. 1200m, 12.08.1990, 1M macropt., 1F brachypt.; west Puerto San Glorio (Prov. Leon), 1620m, 12.08.1990, 1M brachypt.; Sierra de Pela, east of Villacadima (Prov. Guadalajara), ca. 1300m, 23.08.1990, 1F brachypt.; south of Villacadima (Prov. Guadalajara), ca. 1350m, 23.08.1990, 2MM 4FF brachypt.; Sierra de Cazorla (Prov. Jaen), ca. 1100m, 4.08.1979,

3MM 1F; Sierra de Segura (Prov. Jaen): near Orcera, 3.08.1979, 15MM 9FF; northeast Orcera, 1300m, 3.08.1979, 8MM 3FF; south supra Siles, 1100m, 3.08.1979, 4MM 3FF; Montes Universales (Prov. Teruel) north above Valle de Tajo, 6.08.1978, 1M; Laguna de Marquesado, 1400m, 11.08.1979, 14MM 16FF; Sierra de Albarracin, Fuente de Palomares (Prov. Teruel), ca. 1700m, 25.08.1990, 1M macropt., 2MM 1F brachypt.; Supra Nogueras, ca. 1600m, 14.07.1972, 1M; Megina (Prov. Guadalajara), 1300m, 12.08.1979, 2MM 2FF; Sierra de Gudar (Peñarroya): west of Gudar (Prov. Teruel), ca. 1500m, 4.08.1978, 1F brachypt.; Rio Alfambra, 1450m, 27.08.1990, 2MM 2FF macropt., 11MM 16 FF brachypt.; north of Camarillas (Prov. Teruel), 1300m, 3.08.1978, 2MM 6FF; Fontanete (Prov. Teruel), ca. 1450m, 28.08.1990, 25MM 33FF; 6.10.1998, 2MM 8FF; southeastern Pyrenees, Sierra del Cadi (Prov. Barcelona): Vallcebre, ca. 1300m, 4.08.1990, 1M brachypt.; Saldes, 4.08.1990, 1M 1F brachypt. - France: Roussillon, Dépt. Aude, Corbières, Parahou Grand, ca. 700m, 17.08.1979, 1M macropt.; Dépt. Seine-et-Marne, Forêt de Fontainebleau, 12.08.1989, 1M macropt.; Dépt. Eure, Valley of the Seine: Vernon, 15.08.1989, 3FF (the last two French localities were published before as *K. irregularata* Haupt by REMANE & DELLA GIUSTINA 1991).

## Zusammenfassung

Bei den Taxa der Artengruppe von *Kelisia guttula* (Germar) sind bei den Männchen bekanntlich das Genitalsegment, aber auch das Analrohr und besonders der Aedeagus im Vergleich mit anderen Kelisiinae proportional stark (apomorph) vergrößert: der Aedeagus ist extrem verlängert, sehr dünn und biegsam und reicht, halbkreisförmig gebogen, in Ruhelage kopfwärts bei über die Abdomenmitte hinaus. Als "evolutive Antwort" darauf ist in der inneren ektodermalen Genitalarmatur der Weibchen ein spezielles, ungefähr gleichlanges "Führungsrohr" für diesen langen Aedeagus entwickelt - ein Musterbeispiel sowohl für evolutive Koorganisation als auch für "orthogenetische" Evolution. Die Ursachen für diese spezielle Organ-Weiterentwicklung sind offenbar (noch?) unbekannt, doch scheinen es - anders als in manchen Fällen bei anderen Insektengruppen (z.B. Diptera: Tephritidae) - keine Selektionsfaktoren zu sein, die vom Weibchen auszuführende Funktionen (z. B. Eiablage-Techniken, Spermien-Transport und -Aufbewahrung) betreffen. Da der ectodermale Genitalraum der Weibchen seine Länge beibehält, ist das Führungsrohr für den viel längeren Aedeagus (es beginnt an der Dorsalseite der Genitalöffnung und mündet im Bereich der Aufgabelung zur Bursa copulatrix einer- und dem Ductus communis zu Ovarien und Receptaculum seminis andererseits wieder in den Genitalraum) gegenüber dem Genitalraum stark verlängert, von ihm abgefaltet und in  $\pm$  komplizierten Windungen im Abdomenende untergebracht (bleibt aber durch ein dünnes Ligament über seine gesamte Länge mit dem Genitalraum verbunden). Dieses Führungsrohr besitzt Stellen stärkerer und solche schwächerer Chitinisierung. Obwohl bei derartig komplizierten, "hoch organisierten" Strukturen der Verdacht auf das Vorliegen einer "Schlüssel-Schloss-Funktion" zur Verhinderung artfremder Paarungen nahe liegt, scheint eine solche Funktion hier unwahrscheinlich: artfremde Paarungen werden bereits vorher durch die Kommunikation der Partner mit art-spezifischen Vibrationssignalen verhindert, die als "premating isolating mechanism" wirken. Da es aber in der *K. guttula*-Gruppe mehrere Artengruppen gibt, deren Taxa sich in Gestalt, Proportionen, Färbung und Zeichnung so ähnlich sind, dass die Weibchen bisher nicht bis zur Art bestimmt werden konnten (mit allen negativen Folgen für biogeographische und ökologische Analysen), lag es nahe, diese komplizierte innere



ektodermale Genitalarmatur der Weibchen auf artspezifische Merkmalsausprägungen zu untersuchen. Wie wir feststellen konnten, gibt es solche artspezifischen Merkmalsausprägungen besonders im Bereich des "Führungsrohrs" (in seiner Länge, seiner Lage, aber auch in Form, Lage und Grösse der stärker chitinierten Bereiche), so dass nunmehr alle Weibchen der *K. guttula*-Gruppe bis zur Art bestimmbar sind. Dabei zeigte sich, dass die bisher zu der zentraleuropäischen *K. irregulata* Haupt gestellten Populationen aus Spanien und der Westhälfte Frankreichs sich morphologisch so deutlich von den zentraleuropäischen unterscheiden, dass wir hier einen eigenen Genpool annehmen müssen und sie - bis zum Beweis des Gegenteils - als eigenständige, zu *K. irregulata* allopatrisch verbreitete Morphospezies betrachten und beschreiben: *Kelisia occirrega* nov. spec. (Typus - Fundort: Spanien, Prov. Pamplona, Südwest-Pyrenäen, Isaba im Valle del Roncal). Nur falls in der derzeit vorhandenen "Verbreitungslücke" zwischen den beiden Taxa im Osten Frankreichs als Hybride deutbare Exemplare gefunden werden sollte, schiene eine Herabstufung des westlichen Taxons auf Subspezies-Rang erforderlich.

## Riassunto

Nel corso dell'evoluzione, i taxa appartenenti al gruppo monofiletico di *K. guttula* (Germar) hanno acquisito, nelle strutture ectodermiche dei genitali esterni ed interni, sia maschili che femminili, caratteristiche particolari rispetto ai taxa "plesiomorfi" della sottofamiglia Kelisiinae. I maschi delle specie di quel gruppo possiedono rispetto alle dimensioni del corpo un segmento genitale molto ampio ed un edeago molto lungo, sottile e flessibile. "Coorganizzato" con la lunghezza dell'edeago, le femmine hanno sviluppato nei loro genitali interni uno speciale dotto, pressochè della lunghezza dell'edeago, che accoglie e dirige l'edeago durante la copulazione. Questo "dotto edeagale", che deriva dalla parete dorsale della camera genitale, è considerevolmente più lungo di questa ed, in alcuni taxa, forma un lobo largo e ondulato. Esso inizia alla base della camera genitale, decorre dorsalmente a questa e termina di fronte all'origine dell'oviductus communis che conduce alla spermateca e agli ovari. Il dotto edeagale rimane connesso per tutta la sua lunghezza alla camera genitale attraverso un sottile ligamento e è provvisto di varie aree sclerificate. Quel particolare processo di "coorganizzazione" presentato dai taxa del gruppo di *K. guttula* (Germar) potrebbe essere interpretato come un meccanismo atto a prevenire la copula fra individui di specie diverse, ma un meccanismo di isolamento precopula è già presente in questi insetti ed è rappresentato dall'emissione di segnali vibratori specie-specifici che si diffondono tramite il substrato. Finora non siamo riusciti ad individuare un fattore che possa aver favorito quella specializzazione. Nessuna particolare funzione delle femmine, come ovideposizione, o "sperm handling", sembra aver agito, come è avvenuto in altri gruppi di insetti, per esempio nei Tephritidae, come forza selettiva su quelle strutture inducendo quella particolare specializzazione. Le strutture ectodermali dei genitali maschili e femminili sono state esaminate anche per individuare caratteri che permettono di identificare facilmente non soltanto i maschi, ma anche le femmine. Si è così osservato che le femmine di tutti i taxa appartenenti al gruppo *K. guttula* (Germar) presentano caratteri specie-specifici a livello delle strutture ectodermiche dei genitali interni. L'esame di quelle strutture ha permesso di mettere in evidenza nell'ambito di "*K. irregulata* Haupt" due morfotipi allopatrici. Le differenze riscontrate fra le popolazioni della Spagna e della Francia occidentale e quelle dell'Europa centrale

ci hanno indotto ad attribuire le prime due popolazioni ad una specie nuova descritta col nome di *K. occirrega* n.sp..

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Author's address:

Prof. Dr. R. Remane

Fachbereich Biologie (Zoologie)

der Philipps Universität Marburg

Lahnberge, Karl v. Frisch Str.

D-35032 Marburg

Germany

Dr. A. Guglielmino

Dipartimento di Protezione delle Piante

Università della Tuscia

Via S. Camillo de Lellis

01100 Viterbo

Italy

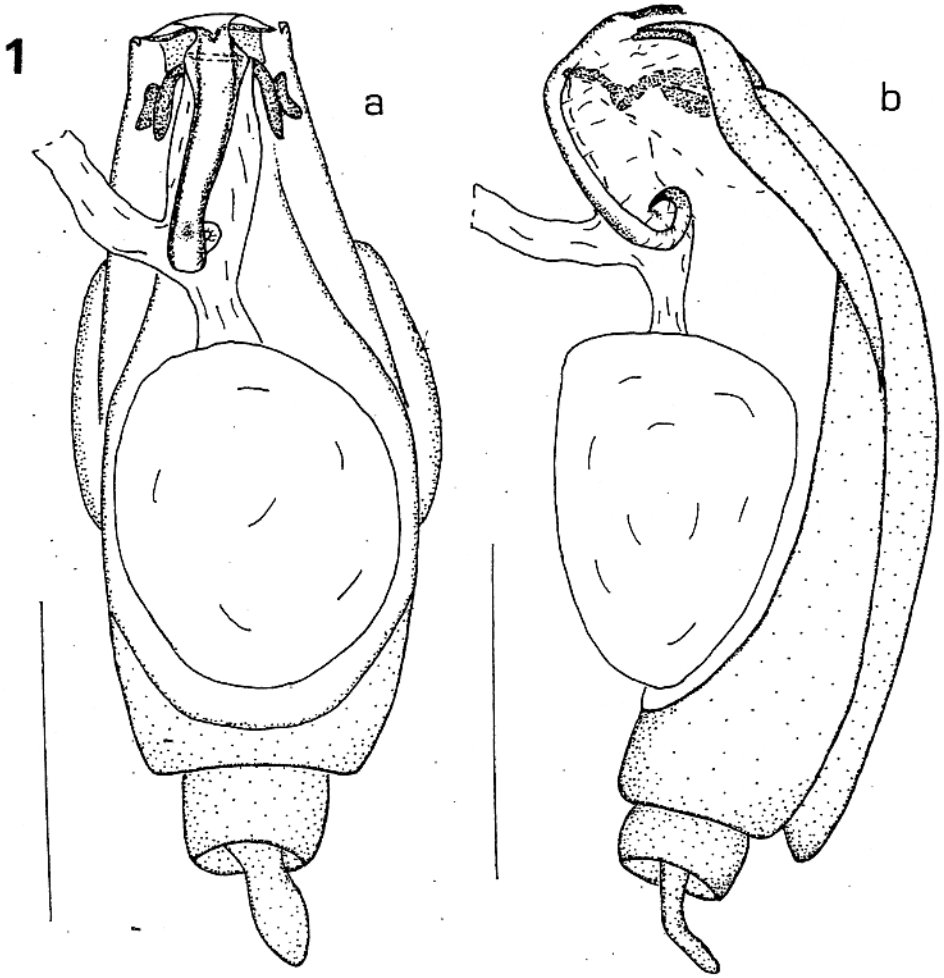


Fig. 1. *Kelisia hagemini* Remane & Jung (specimen from Croatia-Istria: Kozina) Female ectodermal genitalia. a: dorsal view; b: lateral view. Scale: 0.5 mm.

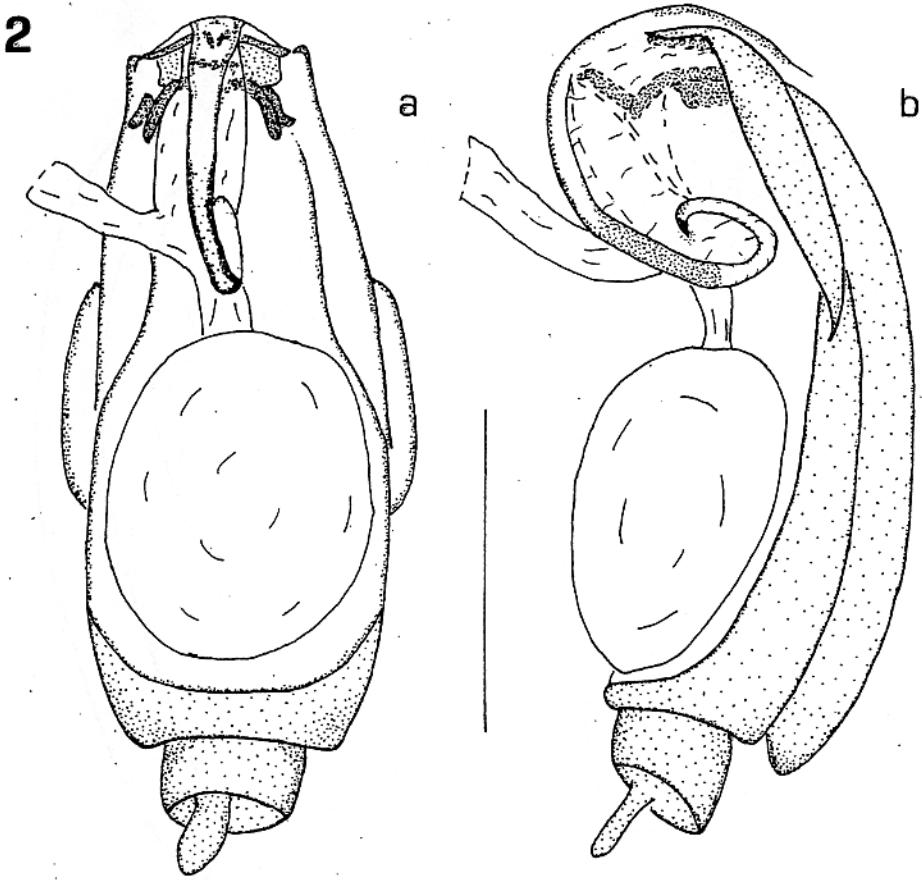


Fig. 2. *Kelisia haupti* Wagner (specimen from Germany, Bavaria: Wollbach): Female ectodermal genitalia. a: dorsal view; b: lateral view. Scale: 0.5 mm.

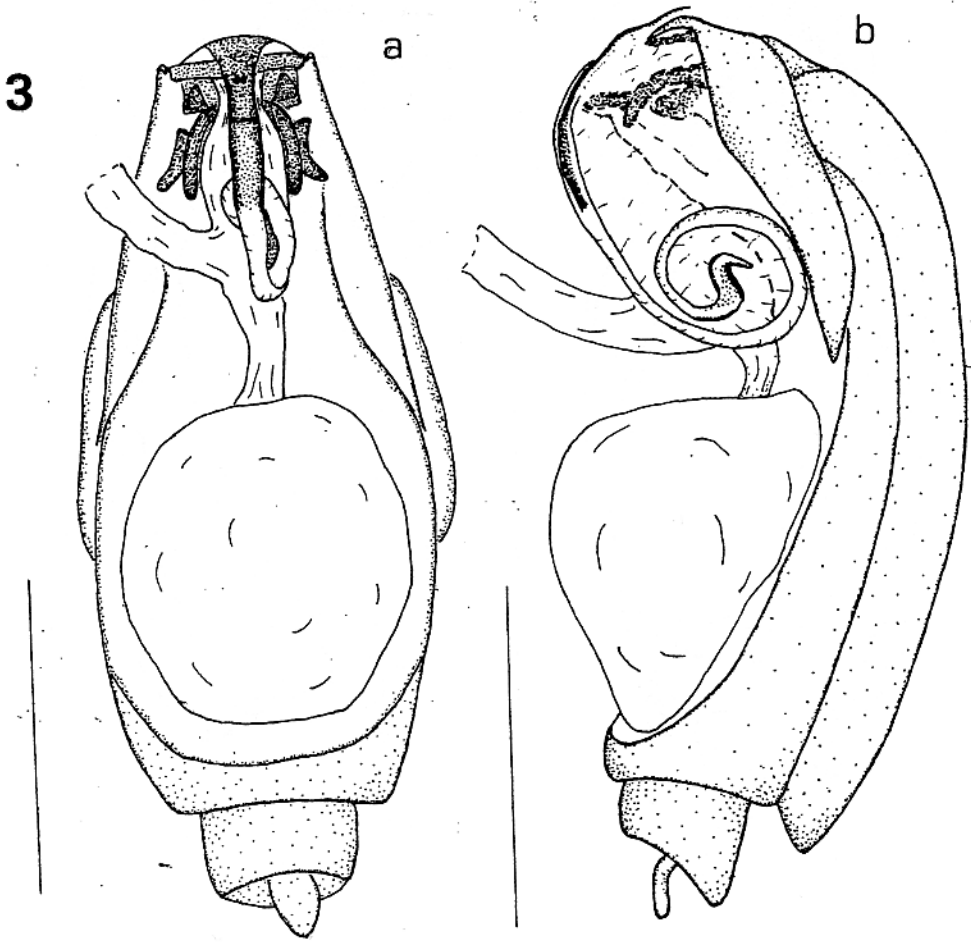


Fig. 3. *Kelisia halpina* Remane & Jung (specimen from Austria-Tirol: Mils): Female ectodermal genitalia. a: dorsal view; b: lateral view. Scale: 0.5 mm.

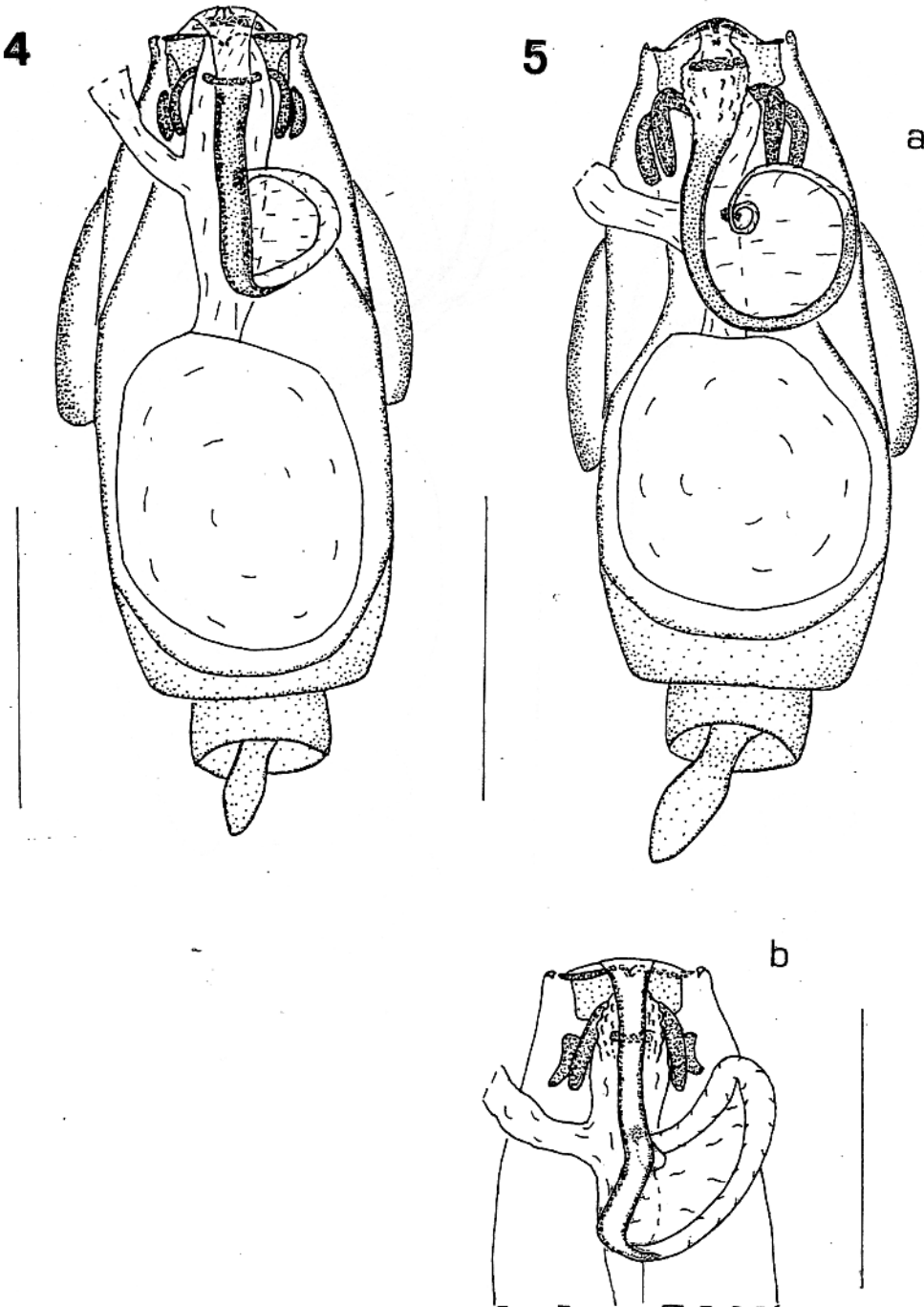


Fig. 4. *Kelisia guttula* (Germar) sensu Wagner (specimen from Germany, Nordrhein-Westfalen: Lengerich): Female ectodermal genitalia: dorsal view. Scale: 0.5 mm.

Fig. 5. *Kelisia sima* Ribaut. Female ectodermal genitalia. a: dorsal view (specimen from Germany, Hesse: Marburg); b: dorsal view (specimen from Germany, Bavaria: Breitbrunn). Scale: 0.5 mm.

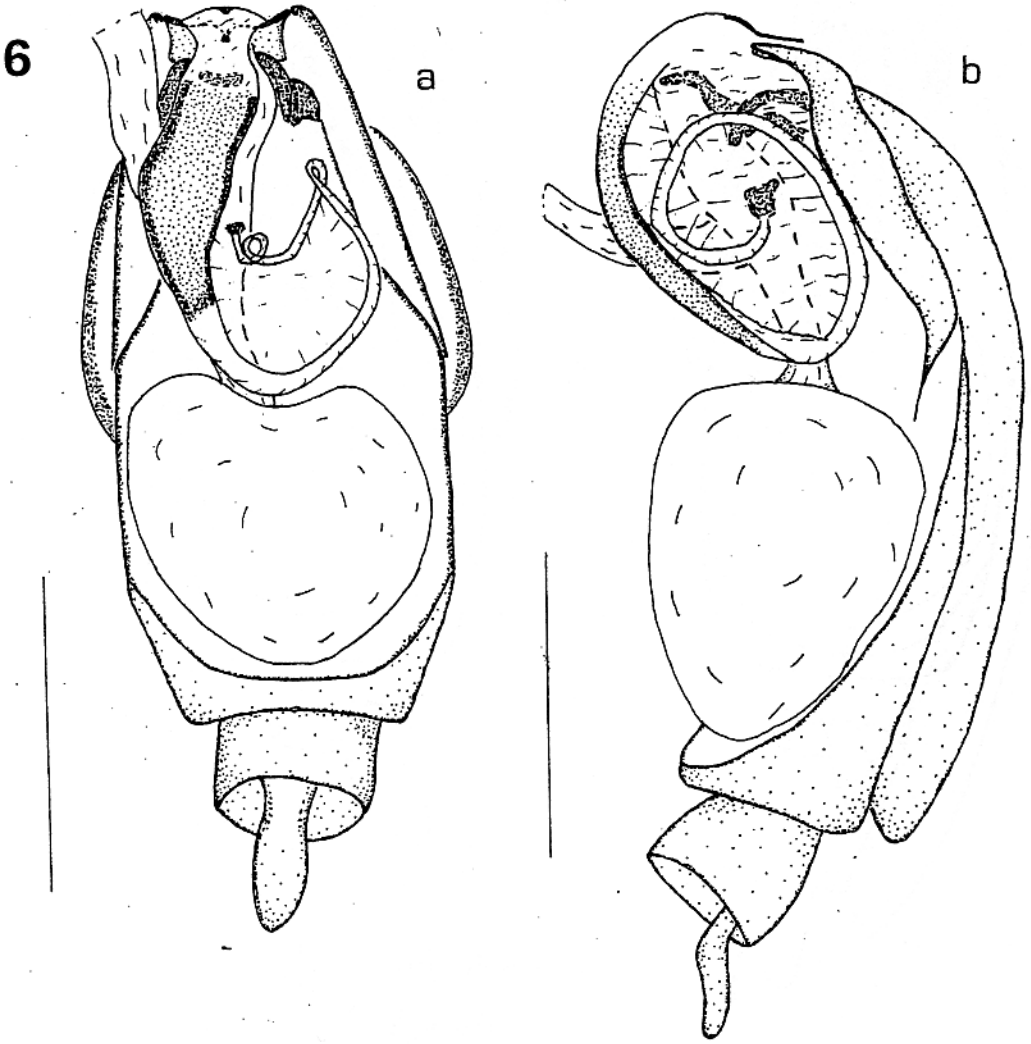


Fig. 6. *Kelisia italica* Guglielmino & Remane (specimen from Italy-Lazio: Monte Terminillo): Female ectodermal genitalia. a: dorsal view; b: lateral view. Scale: 0.5 mm.



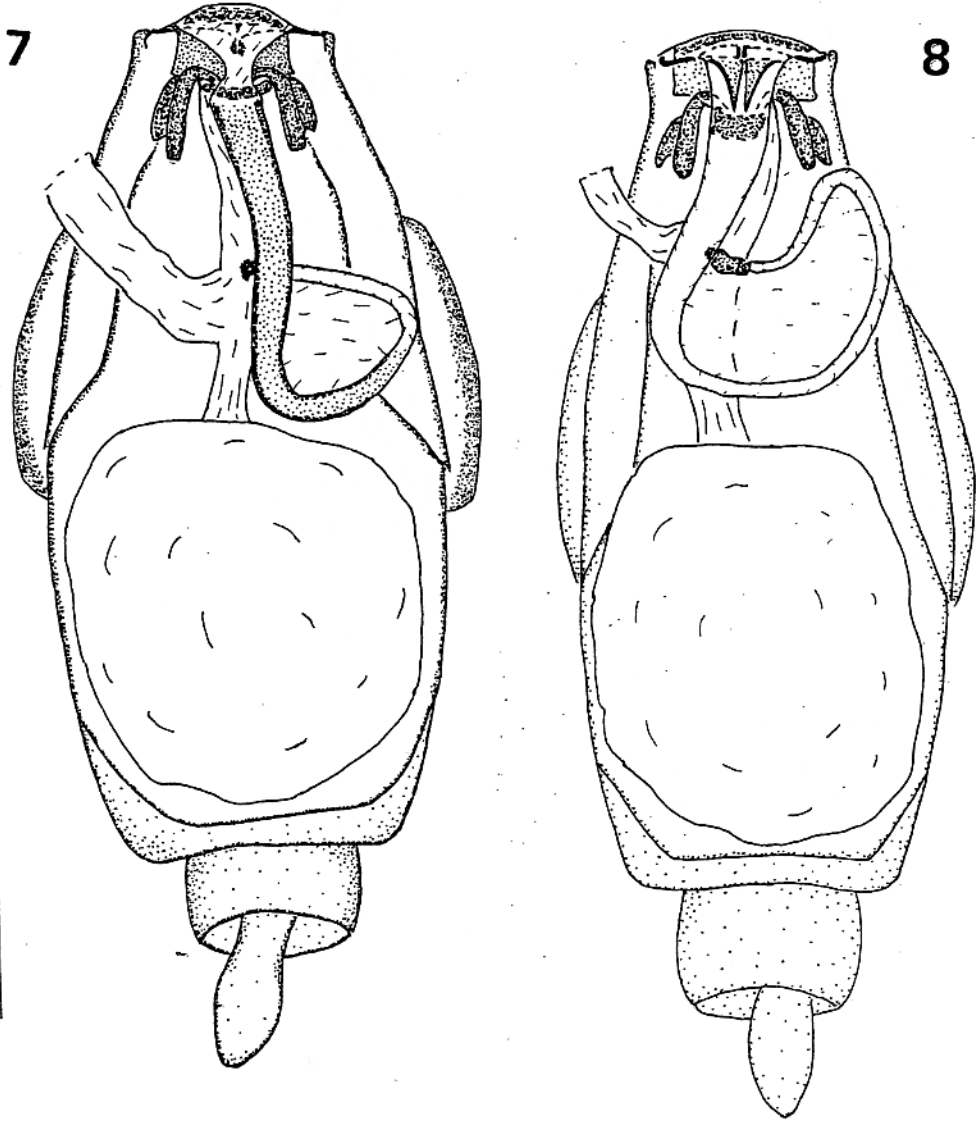


Fig. 7. *Kelisia vittipennis* J. Sahlberg (specimen from Germany, Niedersachsen: Oldenburg): Female ectodermal genitalia: dorsal view. Scale: 0.5 mm.

Fig. 8. *Kelisia irregulata* Haupt (specimen from Germany, Nordrhein-Westfalen: Lengerich): Female ectodermal genitalia: dorsal view. Scale: 0.5 mm.

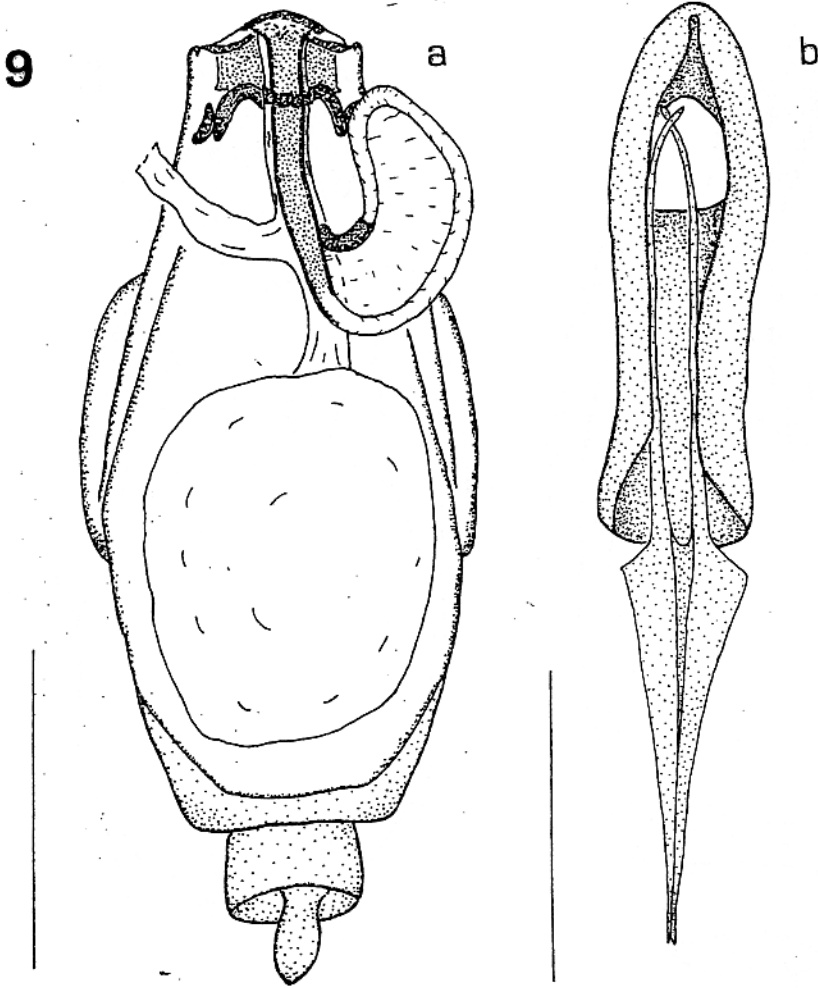


Fig. 9. *Kelisia occirrega* n. sp.

a: Female ectodermal genitalia: dorsal view (Paratype: specimen from Spain, Teruel: Fontañete).

b: Male: Anal appendages and anal tube: ventral view (Holotype: specimen from Spain, Pamplona: Valle de Roncal, north of Isaba). Scale: 0.5 mm.