Diagnostic characters of *Xysticus cristatus*, *X. audax* and *X. macedonicus* (Araneae: Thomisidae)

Elke Jantscher
Institute of Zoology,
Karl-Franzens-University Graz,
Universitätsplatz 2, A-8010 Graz, Austria

Summary

Diagnostic characters of males of the problematic crab spider species *Xysticus cristatus* (Clerck, 1757) and *X. audax* (Schrank, 1803) from central Europe are presented in conjunction with those of a third, very similar species, *X. macedonicus* Silhavý, 1944. Diagnostic characters of the females are also proposed, although not all specimens can be unequivocally placed into one of the three species. The principal diagnostic features of the males are their different emboli: long and thin with a tip divided into two small parts in *X. cristatus*, broad and twisted in *X. audax* and *X. macedonicus*, with a characteristically broadened and feather-like tip in the latter species. Females are distinguished by the shape of the epigynes (genital atria) and internal structures.

Introduction

In previous studies of *Xysticus cristatus* (Clerck, 1757) and *X. audax* (Schrank, 1803) there have always been difficulties and confusion concerning the separation of these two evidently similar and closely related species. Some problems of identification may derive from the occurrence of a third, very similar, though long neglected species, *X. macedonicus* Silhavý, 1944, although extremely high variability, especially among the females, must be considered the main source of confusion.

The aim of the present work is to provide detailed descriptions of diagnostic characters for the unequivocal identification of the males of *X. cristatus*, *audax* and *macedonicus* and to attempt to provide further clarification of the diagnostic characters of the females.

Material and methods

As part of a wider revision of the genus *Xysticus* in central Europe, approximately 470 specimens of *X. cristatus*, 240 of *audax* and 50 of *macedonicus* were examined. A genital preparation was made for about half the females. All of this material was preserved in 70% ethanol and most belonged to different European museum collections (Natural History Museum Berne, Natural History Museum Basel, Natural History Museum Vienna, Stockholm Museum of Natural History, Zoological Museum Berlin). The *X. macedonicus* material examined came from the following private collections: CCD, CPH, CCK, CCM (see below).

The specimens were studied and drawn (hairs omitted in all drawings) using a Wild M8 binocular microscope, while an Olympus BH-2 microscope with interference contrast was used for higher magnification. To avoid any artefacts in the internal structures I refrained from using any chemicals on the specimens to gain a better view of the vulva. All measurements are in mm.

Abbreviations: Fe=femur, Pa=patella, Ti=tibia, Mt=metatarsus, LI–IV=legs I to IV, BL=total body length, PL=prosoma length, PW=prosoma width, PE/AME=ratio of distance PME–PLE/diameter of one AME, AE/AME=ratio of distance AME–ALE/diameter of one AME, AME/AME=ratio of distance between AME/diameter of one AME. Collections: NHMB=Natural History Museum Basel, ZMB=Zoological Museum Berlin, CTB=Theo Blick, CCD=Christo Deltshev, CPH=Peter Horak, CEJ=Elke Jantscher, CCK=Christian Komposch, CCM=Christoph Muster, CVR=Vygandas Relys.

Existing taxonomic problems—historical background

Simon (1932) differentiated the males of *X. cristatus* and *X. audax* on the proportions and shapes of the tegular apophyses (basal and median). In his identification key the females were mainly separated by colour, and the size and distance apart of two dark spots (spermathecal apodemes) near the epigastric fold. Furthermore, different colour patterns were described. Tullgren (1944) used the form of the T-shaped median apophysis and the basal tooth on the lateral apophysis of the male palp to separate them. Females were distinguished by colour and by the shape of the genital atria, resembling a "C" in *X. cristatus* and being variable in *X. audax*. He also figured the variable forms of a few *X. audax* epigynes.

In the same year Silhavý (1944) published a paper on the thomisids (including philodromids) living in the Balkans (mountains in Macedonia and Dalmatia), reporting 36 species. This publication contains the first descriptions of *X. macedonicus* Silhavý, 1944 and *X. tenebrosus* Silhavý, 1944 (the latter is not included in the *X. cristatus*-group and therefore not discussed here) as well as new species of the genus *Philodromus*. Despite the description of the new species with a short synopsis and a version of the title in Latin, this Czech publication has remained almost unknown. It is listed in Roewer (1955) but was not cited by subsequent authors such as Heimer & Nentwig (1991) in their *Spinnen Mitteleuropas*, perhaps due to the locality of the species being too far from central Europe and the fact that only one specimen had been collected. *Xysticus macedonicus* was described as being very similar to *X. audax* in overall colour and shape, with the main differences being in the palpal bulb (Silhavý, 1944: 91–92). Here the median tegular apophysis (shaft thinner than in *X. audax*, prolateral branch of median apophysis three times longer than retrolateral branch—my translation) and the size of the tutaculum (broader and more triangular than in *X. audax*—my translation) were mentioned.

Locket & Millidge (1951: 180) in their respected *British Spiders* stated that *X. cristatus* and *X. audax* are very similar and that the female epigynes are "not distinguishable with any certainty". However, they refer

to several characters to distinguish the two species. These include, in particular, colour patterns (*X. audax* darker and with less distinct wedge-shaped pattern on the carapace), but also genital-morphological differences in the males since they observed (correctly) that in *X. cristatus* the basal tooth on the lateral apophysis is smaller than that of *X. audax*.

Despite his earlier publication (Palmgren, 1950) in which he suggested that *X. cristatus* and *X. audax* simply represent the extremes of a single line of variation, Palmgren (1983) was the first to point out clear differences between the males. He correctly recognised and described the different shape of the distal part of the embolus and provided illustrations of both species. For the separation of females he assumed that examination of the vulva would be necessary, depending on the length and curvature of the canal connecting the receptacula with the copulatory opening. This canal appeared to be shorter and less curved in *X. audax* than in *X. cristatus*, though he stated that in some cases the length of the canal is not a reliable character for an unequivocal identification.

Roberts (1985) also referred to the wedge-shaped pattern and carapace colour for the separation of *X. audax* and *X. cristatus*, although in his drawings of the male palps the much better character of the distal part of the embolus is clearly figured. The drawings of the females are excellent and some of the diagnostic epigynal characters discussed later in the present publication are distinctly shown.

Heimer & Nentwig (1991: 478) listed *X. audax* and *X. cristatus* separately, but said that "Wegen der hohen innerartlichen Variabilität beider Arten wird *audax* oft auch als Varietät von *cristatus* aufgefasst (. . . due to the high intraspecific variability of both species *X. audax* is sometimes interpreted as a variety of *X. cristatus*—my translation). The males were separated by the proportions and shape of the median apophysis, the females by the epigyne and colour.

Other authors, e.g. Holm (1958), also recognised differences in the most distal part of the embolus. Braun & Rabeler (1969) cited Thaler (1966) who had previously stated that the terminal part of the embolus could be used as a diagnostic character. Ono (1988) also stated that *X. audax* is very closely related to *X. cristatus*, but that the males are distinguishable by the shape of the distal part of the embolus.

Results and discussion

Habitat

Xysticus audax and *X. cristatus* are common Palaearctic species with a wide geographical distribution. *Xysticus macedonicus* was originally described from Jablanica-Rujana, Bielo Brdo, a locality in western Macedonia. Nearly 50 years later, Deltshev (1990) recorded *X. macedonicus* for the first time in the Pirin Mountains, Bulgaria, close to Macedonia, and Deltshev & Blagoev (1997) considered it to be a mountain element, endemic to the Balkan Peninsula. Horak (1988) was the first to collect *X. macedonicus* in Austria at xerothermic localities in two steep-sided gorges in Styria (Weizklamm, Raabklamm). Other discoveries in Austria followed later from localities in Carinthia (e.g. Steinberger, 1988; Komposch & Steinberger, 1999), Styria (Kropf & Horak, 1996) and Tyrol (Thaler, 1997). The most recent records of *X. macedonicus* come from the Bavarian Alps (Karwendel). A publication on the first record of this species in Germany with further information is in preparation (C. Muster, pers. comm.). Further occurrences of *X. macedonicus* can be expected in the future and the revision of existing *X. audax* material might also contribute further to the knowledge of its distribution.

All three species can occur sympatrically in one sampling site (e.g. Raabklamm and Weizklamm in Austria). Both *X. audax* and *X. cristatus* are considered to be euryzonal (Thaler, 1997). Deltshev & Blagoev (1997) collected *X. macedonicus* from higher altitudes in montane coniferous and subalpine regions, but this species can also be found at lower altitudes (e.g. at Trögener Klamm, Carinthia, Austria, *c.* 740 m a.s.l.) in sparsely vegetated and rocky habitats. For further ecological data see Braun & Rabeler (1969), Komposch & Steinberger (1999), Maurer & Hänggi (1990) and Thaler (1997).

Colour

In general it is evident that colour is highly variable and ranges from cream-beige to dark black-brown. The patterns of coloration also show great variability. The present study of about 700 specimens supports the idea that there is a slight tendency for *X. cristatus* to be lighter in colour than *X. audax* and *X. macedonicus*. However, some very dark specimens, on first appearance assumed to be *X. audax*, turned out to be *X. cristatus*, and vice versa. *Xysticus macedonicus* males usually have a dark brown prosoma and dorsal side of the legs, while females are mainly brown to slightly olive-brown. Particular colour patterns, such as the wedge-shaped mark on the carapace, vary a lot and different types are not limited to one species. It must be remembered that the examined material had been preserved in ethanol, sometimes for over a hundred years, and this certainly contributes to fading of the colours. Living or recently collected specimens may show more intense and/or slightly different colours.

Leg spination

The investigation of leg spination, carried out on 64 specimens, leads to the conclusion that the distribution of spines follows a roughly similar pattern in all three species but, like coloration, is variable. This variability is manifested in the fact that spination can be different on the right or left side even in a single animal. Normally the spines are positioned in rows and on the ventral side of the tibia and metatarsus in double rows. I have observed that males have more and stronger spines on

	X. audax	*X. cristatus*	*X. macedonicus* (*n*=14)
BL	(*n*=23): (3.5) 4.0 (4.6)	(*n*=22): (3.5) 4.4 (5.6)	(4.7) 5.3 (5.9)
PL	(*n*=22): (1.9) 2.3 (2.7)	(*n*=22): (1.9) 2.2 (2.6)	(2.3) 2.5 (3.0)
PW	(*n*=22): (1.9) 2.2 (2.7)	(*n*=15): (2.0) 2.5 (2.8)	(2.2) 2.5 (2.9)
PE/AME	(*n*=23): 2.1	(*n*=23): 2.6	2.7
AE/AME	(*n*=23): 4.7	(*n*=23): 4.8	4.9
AME/AME	(*n*=6): 4.4	(*n*=6): 5.1	4.6

Table 1: Measurements and proportions of *Xysticus* species: males. Mean, minimum and maximum measurements; *n*=number of specimens examined.

	X. audax (*n*=24)	*X. cristatus*	*X. macedonicus* (*n*=18)
BL	(4.6) 5.8 (7.2)	(*n*=15): (4.7) 5.8 (7.4)	(4.3) 6.0 (7.7)
PL	(1.8) 2.4 (2.9)	(*n*=15): (2.3) 2.5 (3)	(2.3) 2.6 (3)
PW	(2.0) 2.5 (2.8)	(*n*=15): (2.0) 2.5 (2.8)	(2.2) 2.5 (2.9)
PE/AME	2.5	(*n*=16): 3.1	2.9
AE/AME	5.4	(*n*=16): 6.0	5.4
AME/AME	(*n*=2): 5.2	(*n*=3): 6.5	5.0

Table 2: Measurements and proportions of *Xysticus* species: females. Mean, minimum and maximum measurements; *n*=number of specimens examined.

the prolateral and dorsal sides of femur I than females. Examples for all three species are given below. Order of counting: number of spines on dorsal–prolateral–ventral–and retrolateral side of each leg, "+" indicates double rows of spines, "0" indicates that there are no spines present and "w" that the spines are weaker than usual:

X. audax—1♂ (NHMB 727b, Switzerland, Luzern, Vitznau)
Fe: LI 5-8-0-0, LII 5-0-0-0, LIII 5-0-0-0, LIV 6-0-0-0
Pa: LI 0-1-0-0, LII 0-1-1-1, LIII 0-0-0-1, LIV 0-0-0-0
Ti: LI 0-3-4+4-4, LII 0-3-4+4-3, LIII 2-2-3+3-2, LIV 1-3-3+2-3
Mt: LI 0-3-3+3-2, LII 0-3-4+3-3, LIII 0-3-2+2-3, LIV 0-3-1+1-2

X. audax—1♀ (NHMB 727t, Slovakia)
Fe: LI 4-0-0-0, LII 1-0-0-0, LIII 1-0-0-0, LIV 1-0-0-0
Pa: LI 0-0-0-0, LII 0-0-0-0, LIII 1-0-0-0, LIV 2w-0-0-0
Ti: LI 1-1-6+4-0, LII 2w-0-3+3-0, LIII 2-0-3+2-0, LIV 2-0-2-0
Mt: LI 0-2-5+4-1, LII 0-3-5+4-1, LIII 0-2-2+2-2, LIV 0-2-2+1-0

X. cristatus—1♂ (ZMB 8644, Slovakia)
Fe: LI 4-12-0-0, LII 5-0-0-0, LIII 5-0-0-0, LIV 4-0-0-0
Pa: LI 0-1-0-1, LII 0-1-1-1, LIII 1w-0-0-1, LIV 0-0-0-1
Ti: LI 0-3-4+4-3, LII 0-3-4+4-3, LIII 2-2-3+3-2, LIV 2-2-3+3-2
Mt: LI 0-3-4+3-2, LII 0-3-4+3-2, LIII 0-3-2+2-2, LIV 0-3-2+2-3

X. cristatus—1♀ (NHMB 433w, Slovakia)
Fe: LI 1-5-0-0, LII 1-0-0-0, LIII 1-0-0-0, LIV 1-0-0-0
Pa: LI 0-0-0-0, LII 0-0-0-0, LIII 2-0-0-0, LIV 2w-0-0-1w
Ti: LI 0-0-5+5-0, LII 0-0-4+3-0, LIII 2-1-3+2-0, LIV 2w-2-3-0
Mt: LI 0-3-4+4-2, LII 0-3-4+4-2, LIII 0-3-2+2-2, LIV 0-3-2+1-3

X. macedonicus—1♂ (CPH B80-770, Austria, Styria, Raabklamm)
Fe: LI 5-12-0-0, LII 7-0-0-0, LIII 4-0-0-0, LIV 5-0-0-0
Pa: LI 0-1-1-1, LII 0-1-1-1, LIII 0-0-0-1, LIV 1w-1-0-1
Ti: LI 0-3-5+6-3, LII 0-3-5+5-3, LIII 1w-2-4+3-2, LIV 1-2-3+3-2
Mt: LI 0-3-4+4-2, LII 0-3-4+4-2, LIII 0-3-2+2-2, LIV 0-3-2+2-3

X. macedonicus—1♀ (CCK, Austria, Carinthia, Trögener Klamm, 19 June 1998)
Fe: LI 0-3-0-0, LII 1-0-0-0, LIII 1-0-0-0, LIV 1-0-0-0
Pa: LI 0-0-0-0, LII 0-0-0-0, LIII 0-0-0-0, LIV 0-0-0-0
Ti: LI 0-1-5+4-0, LII 0-3-4+5-0, LIII 2-1-3+2-0, LIV 1-1-3-0
Mt: LI 0-3-4+4-2, LII 0-3-4+5-2, LIII 0-3-2+2-3, LIV 0-3-2+2-2

Body length and proportions

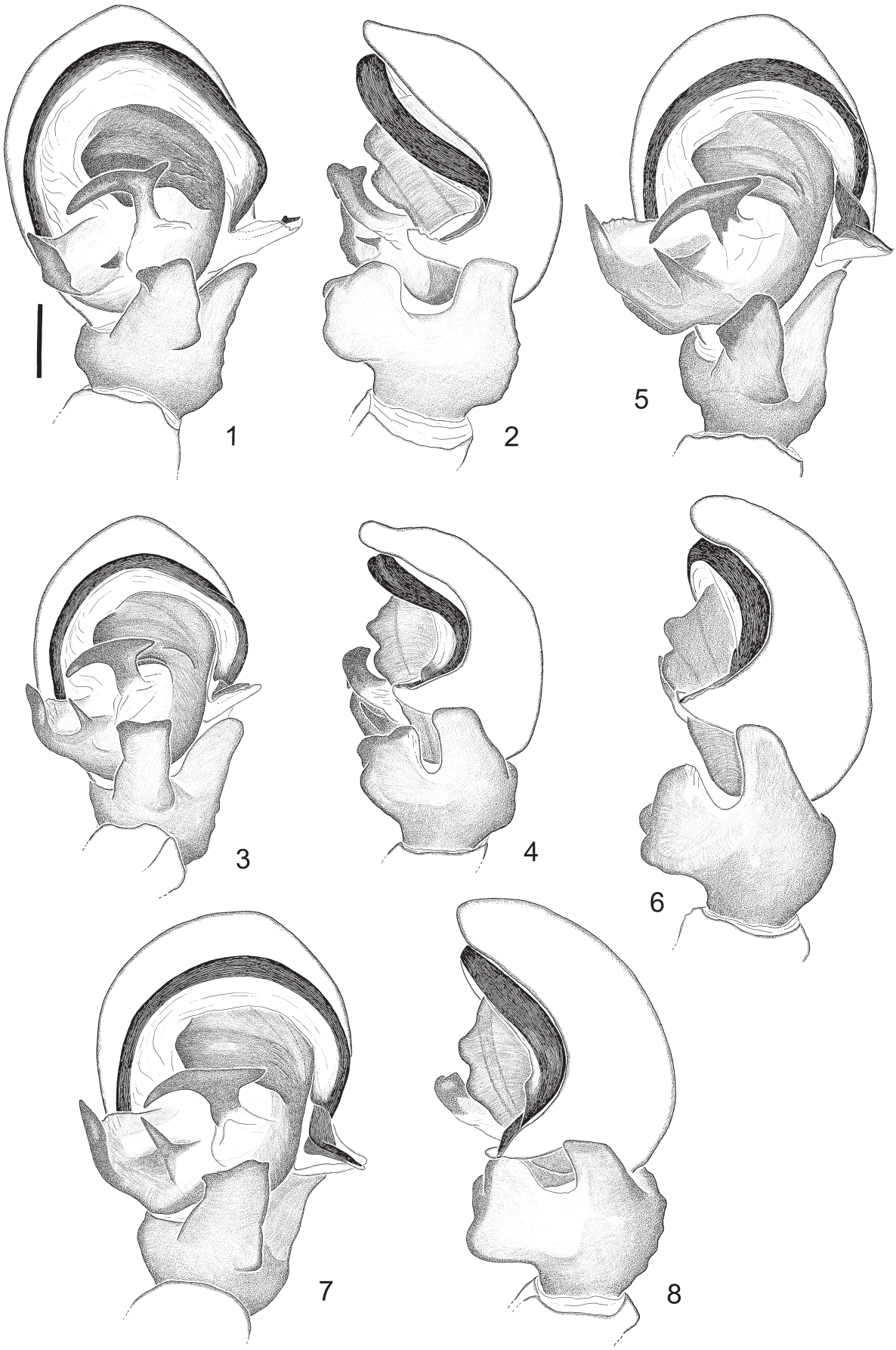
All three species are similar in size, although it seems that *X. macedonicus* tends to be slightly larger than the other two species. Males are usually smaller than females. Examples of different measurements are given for males and females in Tables 1 and 2.

Genital characters: Males

General structure: The overall shape of the bulbus is similar in all three species (Figs. 1, 3, 5). The most prominent parts are the T-shaped median apophysis with two pointed branches, and the broad prolateral apophysis with a distinct pointed tip and a sharp, basal tooth in the basket-like rounded base of the apophysis. The median apophysis has proved to be variable in form and therefore cannot be considered to be a reliable diagnostic character. The embolus is whip-like, elongate and thin. The most distal part of it, lying in the tutaculum, is of a different and characteristic shape in the three species, as described below.

Xysticus cristatus (Figs. 1, 2, 9): The embolus is long and the last third is quite thin and fragile (not directly visible in Fig. 1, but indicated by a dotted line). The terminal part of the embolus is divided into two short protruding parts (Fig. 9): a broader shelf-like more proximal part and a longer and thinner tip at the very end of the embolus. The former points towards the tip of the pedipalp and the latter retrolaterally towards the tip of the tutaculum. Higher magnification shows the distinct shape and also the prominent spination (Fig. 9) on the shelf-like protuberance (Fig. 9: arrow). The basal pointed tooth on the lateral apophysis of the palp is small in *X. cristatus* and therefore easy to overlook.

Xysticus audax (Figs. 3, 4, 10): The embolus is long and the last third is twisted and broad. When removing the embolus from the bulbus with forceps or a needle the



Figs. 1–8: Left male palps. **1–2** *X. cristatus*, CPH, Austria, Tyrol, surroundings of Innsbruck, 590 m a.s.l., 19 May–2 June 1987. **1** Ventral; **2** Retrolateral. **3–4** *X. audax*, CPH, B80-727, Austria, Styria, Raabklamm. **3** Ventral; **4** Retrolateral. **5–6** *X. macedonicus*, Austria, Carinthia, Trögener Klamm, SW Eisenkappel, 1050 m a.s.l. **5** Ventral; **6** Retrolateral. **7–8** *X.* cf. *macedonicus*, CPH, Austria, Upper Styria, top of Stoderzinken, 26 June 1990. **7** Ventral; **8** Retrolateral. Scale lines = 0.2 mm.

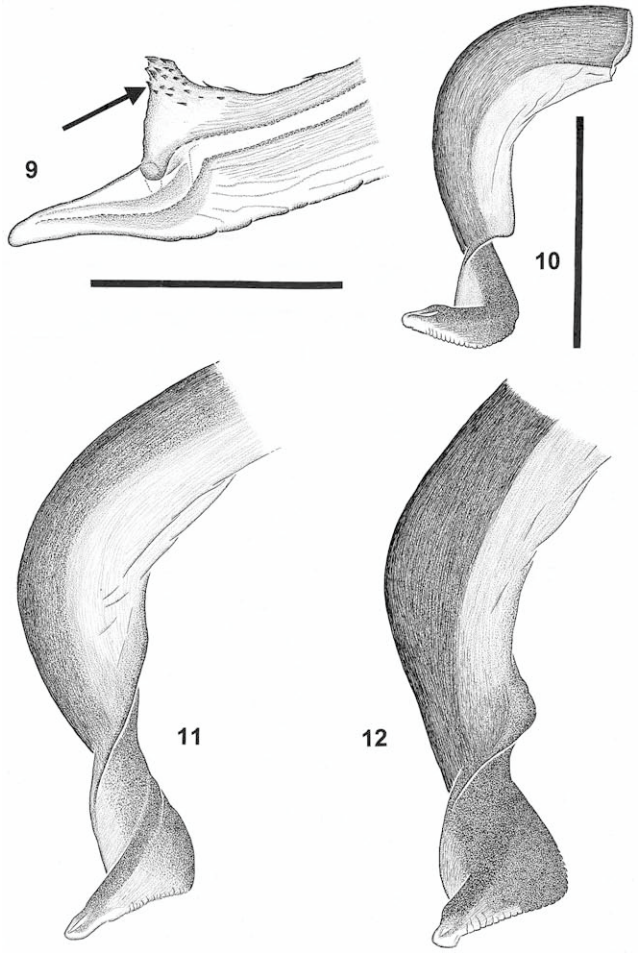
twisted area can be clearly seen in lateral view. This area is marked by a sharp edge (Fig. 10) where the thin and nearly transparent part of the embolus ends and only the dark black, thick part continues. In ventral view the twist is more difficult to see, but is at about the point where the tutaculum begins. The terminal part of the embolus (Fig. 10) is mostly dark and slightly curved; the tip is blunt. The basal tooth on the lateral apophysis is sharply pointed and of considerable length.

Xysticus macedonicus (Figs. 5, 6, 11): The embolus is long and its last third is twisted and broad. The twist is gentle and in lateral view has a sloping edge. It forms part of a larger structure which can, in overall shape, be compared to a feather: a dark "quill" flanked by two wings (Fig. 11). The wings or side-structures are almost entirely black proximally, but distally the structures become increasingly colourless and transparent. Sometimes on first impression of this distal part it seems as if only the median dark part is present and the wings are invisible. In some cases this part has been observed to be almost completely black and rather squat (Figs. 7, 8, 12). It remains to be determined whether this is within the normal range of variability. The basal tooth on the lateral apophysis is sharply pointed and of considerable length.

Genital characters: Females

General structure: The epigyne is characterised by two depressions (genital atria) divided by a median septum. Side-plates—visible bulges of the median septum—of different shapes (structures closely associated with the septum) may be present. In many cases in the material studied one or both atria were sealed with plugs. These are easily removed with forceps or a needle. Halfway between the posterior border of the genital atria and the epigastric fold, typically placed in a transverse fold, two dark spots, representing the area where the spermathecal apodemes (Schick, 1965) are situated, are clearly visible. The receptacula appear to be situated at these points and are lightly attached to the inner side of the opisthosomal cuticle. The size, distance apart, and colour of these spots are variable.

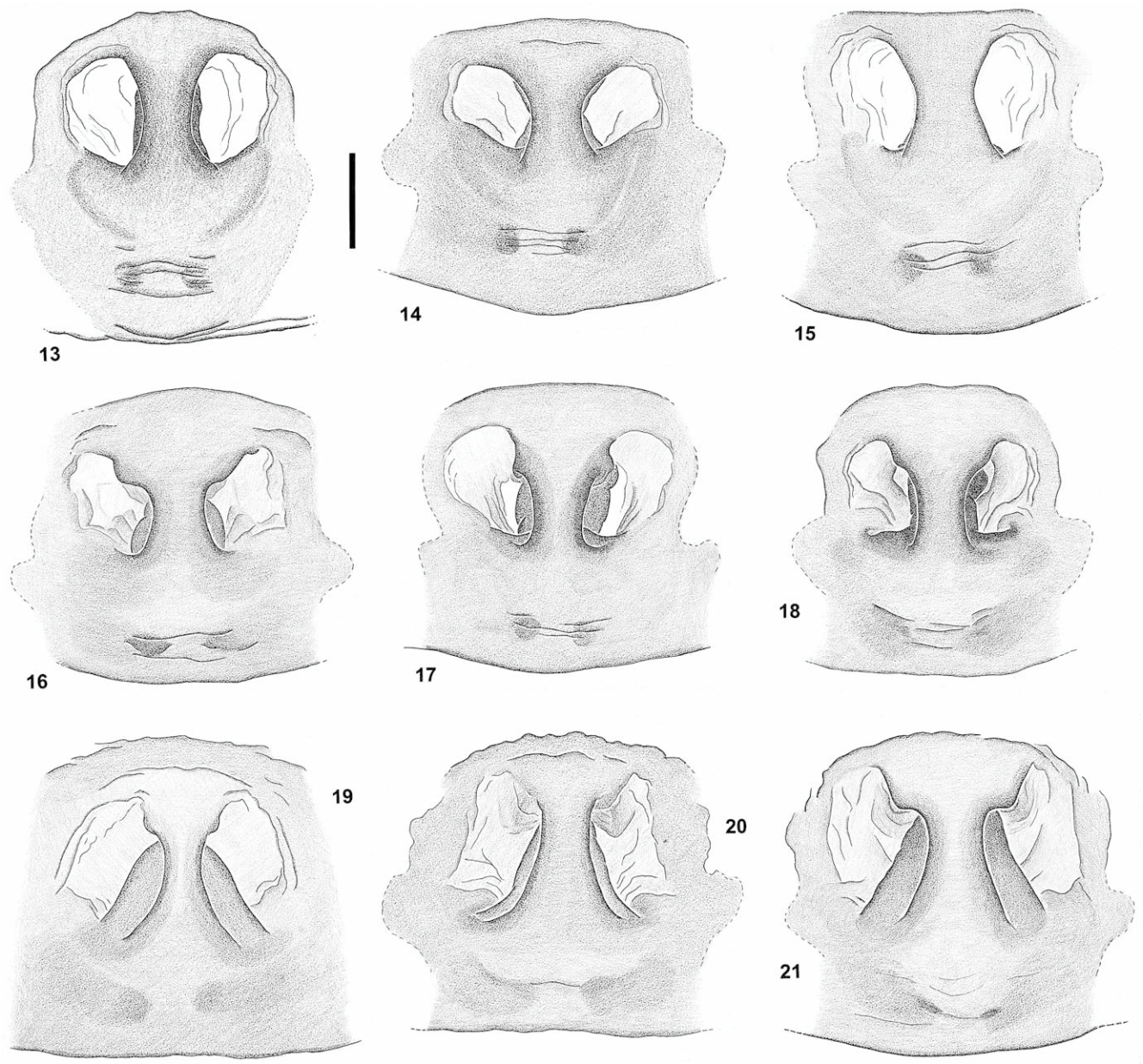
The internal structures of the vulva are highly variable and consist of a number of parts. The oval receptacula are the most striking features, but their size and angle of position are not constant. Under higher magnification an inner compartmentalisation with folded chambers is visible. Very thin fertilisation ducts (which are easily destroyed during the clearing process) are attached to these receptacula. Soft and membranous copulatory ducts connect the receptacula with the genital openings. The latter are normally situated in the anterior third of the epigyne at the deepest point of the base of the epigynal grooves. Inside they open into huge folded, membranous pocket-like structures which are very soft and flexible. Identification primarily depends on study of the copulatory ducts. Typically glands (Figs. 24, 25, 28, 29) are located on the copulatory ducts at a position just anterior to the receptacula. These structures can only be seen under high magnification.



Figs. 9–12: Embolus tips. **9** *X. cristatus*, CEJ, A-S-95-91, Austria, Styria, NNE Grossheimschuh, SW Sulmsee, 270 m a.s.l., 2–29 April 1995, left palp, dorsal; arrow indicates shelf-like protuberance. **10** *X. audax*, CCM, Germany, Karwendel, Soiernspitze, 27 June 1998, right palp, ventral. **11** *X. macedonicus*, CCM, Germany, Mangfallgebirge, Hochmiesing, *c.* 1820 m a.s.l., 10 June 1998, right palp, ventral. **12** *X.* cf. *macedonicus*, CCM, Germany, Mangfallgebirge, Hochmiesing, *c.* 1820 m a.s.l., 10 June 1998, right palp, ventral. Scale lines = 0.05 mm (9), 0.2 mm (10–12).

Xysticus cristatus (Figs. 13–15, 22–24): The shape of the genital atria is smooth and the boundary with the surrounding area is distinctly defined, especially at their posterior margin (Figs. 13–15). The median septum is also regular. Normally side plates are absent, but occur occasionally (Figs. 13, 14). Sometimes dark lines are visible between the dark spots (attachment points of the spermathecal apodemes) and the most outward position of the posterior margin of the genital atria (Fig. 13). The course of these lines is steep and slightly diagonal.

The vulva structures correspond to the general description, although the copulatory ducts are characteristic for this species. The horizontal duct is doubly bent at its most lateral position, located just anterior to the receptacula (Fig. 22). Furthermore, the most anterior part of this curvature is situated at about the mid-point antero-posteriorly along the length of the vulva (i.e. at about the point where the epigynal grooves would begin on the ventral side (Figs. 22–24).

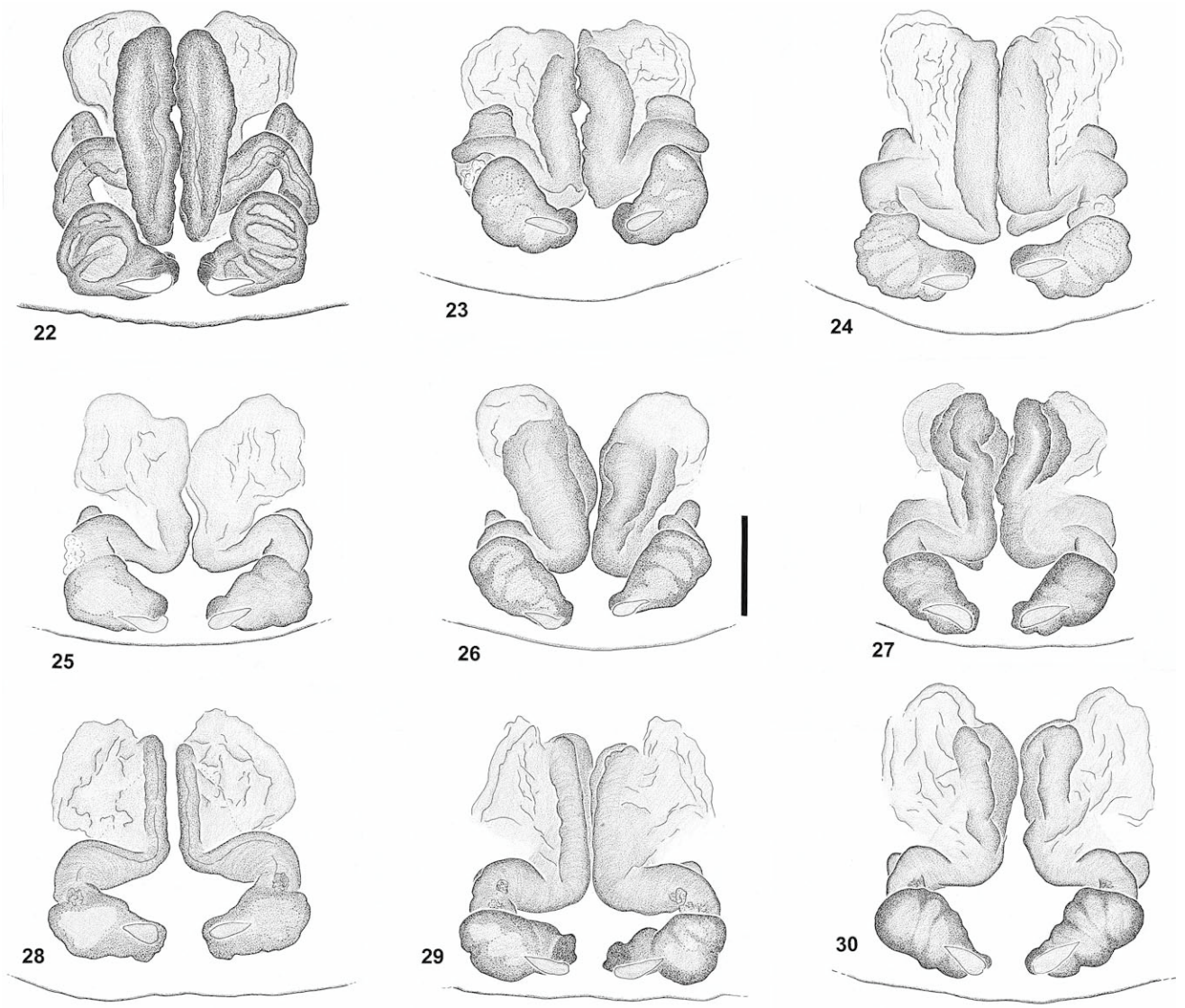


Figs. 13–21: Epigynes, ventral view. **13–15** *X. cristatus*. **13** NHMB 433s, Switzerland, Tessin, Bedretto; **14** CPH, A77-54, Austria; **15** CEJ, A-S-95-79, Austria, Styria, NNE Grossheimschuh, SW Sulmsee, 270 m a.s.l., 2–29 April 1995. **16–18** *X. audax*. **16** CVR, Austria, Gastein, Kötschachtal, 18 August 1994; **17** CTB, Germany, Bavaria, Feuchtwangen, May 1992; **18** CPH, A88-2. **19–21** *X. macedonicus*. **19** CCD, Bulgaria, Pirin Mountain, Prevala, 2400 m a.s.l., 18 July 1978; **20** CCM, Germany, Mangfallgebirge, *c*. 1820 m a.s.l., 10 June 1998; **21** CCM, Germany, Mangfallgebirge, *c*. 1820 m a.s.l., 10 June 1998. Scale lines = 0.2 mm.

Xysticus audax (Figs. 16–18, 25–27): In this species the shape of the genital atria is highly variable and can best be described as ear-shaped (e.g. Fig. 17). The median septum varies, especially at the anterior end. This part sometimes resembles a cup or funnel, sometimes it is similar to the regular median septum of *X. cristatus*. Side-plates are often quite distinct, large and of dark colour (Figs. 16–18). The posterior part of the genital atria is normally bordered by a transverse line beginning at the posterior end of the median septum and continuing laterally. The course of dark lines on the posterior ventral surface, if present, tends to be more horizontal than diagonal. The result is a more or less distinct transverse dark area just behind the genital atria.

The copulatory ducts are very simple (e.g. Fig. 25) with the nearly horizontal duct bending towards the receptacula. Normally they are restricted to the posterior third of the vulva.

Xysticus macedonicus (Figs. 19–21, 28–30): The epigyne (Figs. 19–21) is strikingly different from the other two species. The median septum is quite thin in overall appearance and is narrowest at about one-third of its length from the anterior end. The most anterior part is slightly broadened and shaped like a candelabrum. Elongate, broad side plates are located beside the septum. Their posterior ends are not clearly defined but gradually merge into the normal ventral surface. The internal structures (Figs. 28–30) are like those in *X. audax* and are similarly variable.



Figs. 22–30: Vulvae, dorsal view. **22–24** *X. cristatus*. **22** NHMB 433s, Switzerland, Tessin, Bedretto; **23** CPH, A77-54, Austria; **24** CEJ, A-S-95-79, Austria, Styria, NNE Grossheimschuh, SW Sulmsee, 270 m a.s.l., 2–29 April 1995. **25–27** *X. audax*. **25** CVR, Austria, Gastein, Kötschachtal, 18 August 1994; **26** CTB, Germany, Bavaria, Feuchtwangen, May 1992; **27** CPH, A88-2. **28–30** *X. macedonicus*. **28** CCD, Bulgaria, Pirin Mountain, Prevala, 2400 m a.s.l., 18 July 1978; **29** CCM, Germany, Mangfallgebirge, *c*. 1820 m a.s.l., 10 June 1998; **30** CCM, Germany, Mangfallgebirge, *c*. 1820 m a.s.l., 10 June 1998. Scale lines=0.2 mm.

Conclusions and diagnostic characters

It must be explicitly stated, that colour and colour patterns are not reliable diagnostic characters for the separation of the three species (see also Braun & Rabeler, 1969). In my opinion the only way to make a correct identification is a close investigation of genital-morphological characters. Palmgren's (1983) conclusions about diagnostic characters of *X. audax* and *X. cristatus* (e.g. different shape of embolus, different copulatory ducts) are supported by the results of these investigations. Some of the conclusions of other authors cited above partly contribute to the concept of the species, but are not wholly reliable in their entirety. My results clearly show that Simon's (1932) feature, the distance between the spermathecal apodemes on the ventral side close to the epigastric fold, cannot be considered as a reliable character for identification. Tullgren (1944) correctly used the shape of the genital atria for separation, but considered the T-shaped median apophysis in the males to be a diagnostic feature, something which is not supported by my studies, although it must be added that the basal tooth on the lateral apophysis is, in fact, different in *X. cristatus* and *X. audax*. Locket & Millidge (1951) referred mainly to colour patterns to separate female *X. cristatus* from *X. audax* and to the basal tooth on the lateral apophysis in males. Females cannot conclusively be identified by colour patterns, and the most distal part of the embolus represents a much better character in the males. Even Roberts (1985), whose drawings show precisely the differences between males and females in both *X. cristatus* and *X. audax*, referred to colour patterns. The drawing of the vulva of *X. cristatus* in Heimer & Nentwig (1991: 487, fig. 1256.4) does not correspond with the results of the present study (it could be *X. audax*) and is not useful for identification, although the drawings of the epigynes (figs. 1256.3 and 1257.3) show the main differences quite well.

My data clearly show that males can be distinguished by the different shapes of the embolus and embolus tip, which prove to be reliable diagnostic characters for an unequivocal identification.

The embolus of *X. cristatus* is far thinner and much more fragile than that of the other species. The last third of it is not twisted and the embolus tip is characteristically divided into two small parts which can easily be seen with low magnification under the stereomicroscope (Fig. 9). The basal tooth on the lateral apophysis is very small, whereas it is larger in *X. audax* and *macedonicus*. *Xysticus macedonicus* represents the other extreme with a broad, slightly twisted, feather-like embolus tip and quite a robust embolus (Fig. 11). *X. audax* lies between these extremes with a strikingly twisted embolus and blunt, but not divided, tip (Fig. 10). A comparison of the *X. audax* and *macedonicus* embolus (Figs. 10–11) reveals the similarity in the structure of this genital character.

Some males are somewhat problematic (Figs. 7, 8, 12). Their overall embolus shape is more like *X. macedonicus*, but the wing-like structures are not so distinct and the whole tip is more squat, so that they also resemble *X. audax*. Whether these specimens are simply examples of the range of variability in *X. macedonicus* or whether they are a product of hybridisation or even independent species, remains to be investigated in the light of more material.

Females are more difficult because of the high variability of epigyne and vulva, as can be seen in Figs. 13–30, but three distinct groups based on genital morphology are proposed which correspond to the three species. In about 50% of all cases the removal of the epigyne is necessary to achieve a reliable identification. However, this is not absolutely necessary for identification of *X. macedonicus*. Females of this species show the most distinct characters of the three and their identification is less difficult.

The examination of a large number of females showed that some examples of both *X. audax* and *X. cristatus* are more problematic, and not all females fit easily into one of these proposed groups owing to the extremely high variability of the epigyne and vulva. Characters can differ significantly from those described here, and in such cases an unequivocal identification remains questionable. Perhaps another methodological approach, e.g. closer investigation of ecology, ethology or molecular methods can be used in the future. I propose the following characters which permit the identification of the majority of females:

The posterior margin of the genital atria of *X. audax* is distinctly closed, as in *X. cristatus*, while it is ''open'' in *X. macedonicus*. Side-plates of *X. audax* can be large and broad, while they are absent or small in *X. cristatus* and considerably elongated in *X. macedonicus*. The shape of the median septum and the genital atria is variable (ear-shaped) and not so smooth and regular in *X. audax* as compared with *X. cristatus*. In fact Tullgren's (1944) proposal that the septum/genital atria of *X. cristatus* is ''C''-shaped is supported. *X. macedonicus* has a very thin median septum, with its narrowest part close to the anterior margin of the epigyne. The copulatory ducts of *X. audax* (Figs. 25–27) are simpler and not as massive as in *X. cristatus* (Figs. 22–24). Sometimes only a single duct is visible, sometimes this duct has two bulges at its bend, but this twist never reaches the anterior position that is sometimes seen in *X. cristatus*. The diagnostic feature of *X. macedonicus* is the lack of a clearly defined posterior margin of the genital atria combined with elongated side plates which continue onto the normal, ventral surface of the opisthosoma. Sometimes a slight confining line extending halfway from the median septum is present, but there is no distinct posterior margin. The internal structures of *X. macedonicus* are comparable with those of *X. audax* and cannot be used as diagnostic characters.

It is important to remember that some of the other species of the *cristatus*-group such as *Xysticus ferrugineus* Menge, 1876 or *Xysticus tortuosus* Simon, 1932 are, on first appearances, similar to the three discussed species and could be easily misidentified (especially females). For this reason special attention must be paid to the distinctly different genital characters.

Identification key to *Xysticus audax*, *X. cristatus* and *X. macedonicus*

This key is based on the examined European material and is proposed principally for the identification of males. For the females I have tried to establish those characters which are reliable in the majority of cases, but as mentioned above, these characters are extremely variable and some specimens will not fit easily into this scheme.

Males

1. Embolus tip broad, flanked by two wing-like structures which are increasingly transparent at distal end (Fig. 11) .....*X. macedonicus*
– Embolus tip thin or not especially broadened 2
2. Embolus twisted in its last third, tip blunt and dark, basal tooth on lateral apophysis long and pointed (Fig. 10).....*X. audax*
– Embolus not twisted, thin and delicate, tip split into two parts, basal tooth small and pointed (Figs. 1, 9) .....*X. cristatus*

Females

1. Posterior margin of genital atria not distinct, side-plates distinct and elongated (Figs. 19–21) .....*X. macedonicus*
– Posterior margin of genital atria clearly defined, side-plates irregular, broad or lacking.....2
2. Edges of genital atria regular and smooth, ''C''-shaped, side plates small (Figs. 13–15); vulva with doubly twisted, large copulatory ducts, twisted lateral parts reaching up to mid-point of vulva (Figs. 22–24) .....*X. cristatus*
– Edges of genital atria irregular, ear-shaped, side plates dark, broad (Figs. 16–18); vulva with simple copulatory ducts, lateral parts restricted to posterior third of vulva (Figs. 25–27).....*X. audax*

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