Uncommon conformation of the male palp in common Holarctic spiders belonging to the *Lathys stigmatisata* group (Araneae, Dictynidae)

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Summary

Spiders of the *Lathys stigmatisata* group are rather common throughout the whole of Eurasia and North America. In Europe this group encompasses at least 7 species and is distributed from the south of England to the Mediterranean. Revisional study of this group reveals that the conformation of the male palp of this group is much more complicated than was thought earlier and has several unique features that have never been reported from *Lathys*, Dictynidae and other spider families. The most unique characters are as follows: (1) all architecture of the bulbus is based on spirals and coils; (2) the upper arm of the conductor is coiled and ribbon-shaped; (3) the terminal part of the conductor is totally clamped in position by three tibial apophyses and the cymbium.

Introduction

The spider genus *Lathys* Simon, 1884 belongs to the subfamily Cicurininae (Lehtinen, 1967). It contains 35 species belonging to several species groups. Spiders of the *Lathys stigmatisata* group have a Holarctic distribution. They occur across Eurasia, from Portugal to Chukotka, and in the western Nearctic (Map 1). Around 7 species are known to belong to this group, earlier called the *Lathys puta* group (Lehtinen, 1967; Wiehle, 1967; Ono, 2003), although the real species diversity in this group is at least twice as great (Ovchinnikov *et al.*, in prep.).

Owing to the wide distribution of *Lathys stigmatisata* (Menge, 1869) and related species, and lack of revisions or proper descriptions, we decided to revise the East Palaearctic members of this group (see Ovchinnikov *et al.*, in prep.).

Study of the male copulatory organs in this group reveals several peculiar and even unique structures, and the main aim of this paper is the description of the complicated and unique structure of the male palp in the *L. stigmatisata* group, in comparison with related groups.

Material and methods

In proposing several new terms or using old morphological terms we are not attempting to establish a fixed terminology or the priority of newly invented terms. Our terms are just a formal explanation of various parts of the palp and epigyne, and only some of them can be totally homologised with parts of the palps in other Amaurobioidea (embolus, cymbium, basal haematodocha). Where some terms were previously applied to different parts of the palp we provide short comments.

When we started this project we had insufficient specimens of *L. stigmatisata*, and therefore we used several species belonging to the *stigmatisata* group to illustrate different aspects of the male palp and female epigyne.

Material used in this paper was obtained from the Zoological Museum of the University of Turku and the private collections of Y. M. Marusik and S. V. Ovchinnikov.

Illustrations were made using reflected and transmitted light microscopes equipped with drawing devices. SEM-micrographs were made with a JEOL JSM-5200 in the Zoological Museum, University of Turku. All figures were made from the left palp.

History of delusions

When we began our revision of the *L. stigmatisata* group we thought that the palp was rather simple (see Fig. 1), consisting of (1) a cylindrical (pill-like) tegulum; (2) a screw-like conductor and long coiled whip-like embolus originating from the basal part of the tegulum; and (3) a palpal tibia with two apophyses (dorsal and retrolateral). Our concepts were based on the publications of other authors (Gertsch, 1946; Chamberlin & Gertsch, 1958; Lehtinen, 1967; etc).

Our fourth delusion was connected with the process of copulation. We initially thought that the terminal part of the conductor could move out from the clamp formed by the tibial apophyses during copulation.

Further studies revealed that none of our assumptions was correct (Figs. 9–21): (1) the tegulum is much thinner, and has the shape of a disc in lateral view; (2) the conductor is much more complicated and consists of two arms, one screwed and the other coiled; (3) there are three tibial apophyses; and (4) the conductor cannot disengage from the clamp formed by the tibial apophyses.

Conformation of the male palp

Relatively short. Trochanter-femur length equal to tibia-cymbium length (Fig. 10). Coloration as in carapace and walking legs.

Tibia (Figs. 9–12, 16): Slightly swollen (Figs. 9, 11). Ventral side with short or long furrow (*Tf*). Tibia bears three apophyses (Fig. 16): (1) dorsal (*Da*), with wide base and thin, sharply pointed apical part directed retrolaterally; (2) short finger-like intermediate (dorsolateral) apophysis (*Ra*); and (3) lamellate lateral apophysis (*Va*) with deep or shallow longitudinal furrow (*Vf*). The furrow of the lateral apophysis probably serves to guide the embolus.

Map 1: Distribution of the *Lathys stigmatisata* group.

The tip of the dorsal apophysis can be blunt or sharply pointed (Figs. 12, 16), or very elongate as in *L. teideensis* Wunderlich, 1992. The intermediate apophysis has a small bill-shaped outgrowth on the inner side of the tip, not shown in the figures.

The apophyses, together, form a clamp which holds the screwed part of the conductor in place (Fig. 16b). The screw can rotate slightly, but cannot move forward or backward. None of the hundreds of males observed had the conductor free of the clamp.

A survey of the literature devoted to species belonging to the *L. stigmatisata* group and diagnostic drawings revealed that the presence of the intermediate apophysis has been overlooked. The role of the tibial apophyses in forming a groove "which receives the spiraled portion of the embolic division [embolus+conductor's pedes]" was described for the first time by Gertsch (1946). It seems that the dorsal tibial apophysis was first observed by Wunderlich (1992).

Cymbium (Figs. 9–10, 13): Shape varies from nearly round to elongate. It is rather deep and contains a long basal haematodocha (*Bh*) (Figs. 13, 17); depth can be equal to $\frac{1}{2}$ of cymbial length. Dorsal part of cymbium almost conical. Apical part bears 4–6 macrosetae. Size of apical part varies between species from very short and wide (less than tegulum radius) to long. Basal part of cymbium may have a shallow groove (*Cg*, Figs. 11–12, 16) corresponding in position to the dorsal tibial apophysis.

Subtegulum (*St*, Fig. 21): Small, partly coiled, hidden by tegulum and conductor in ventral view, and by cymbium in dorsal view.

Tegulum (*Te*, Figs. 14–15, 17, 20–21): Discoidal in lateral view (Figs. 15, 17). In dorsal view it appears round or slightly oval-shaped (Fig. 14), but is coiled with a rounded tip (*Tt*) (Fig. 21). The seminal duct (*Sd*) originates (*Ss*) in the subtegulum (Fig. 14), then passes through the tegulum, making slightly more than one coil. Along its course it has one loop (*Sl*). The form of the loop varies, from very deep to shallow. This loop is located on the side opposite (180°) to the base of the embolus (*Eb*), except in one undescribed species.

Conductor (Figs. 9–11, 14–21): Complicated, can be divided into three parts: (1) base (*Cb*); (2) screwed terminal part (*Cs*); and (3) long coiled apical portion (*Cl*1 and *Cl*2). Conductor attached to tegulum by "apical" haematodocha (*Dh*).

(1) Base with large lobe (*Co*) (Fig. 9) directed prolaterally; its prolateral margin membranous (*Cm*). The process of the conductor which is directed downward (posteriorly) we call pedes of conductor (*Cp*). The basal part of the conductor is separated from the apical

portion by a small extension of the upper part of the pedes (*Cu*).

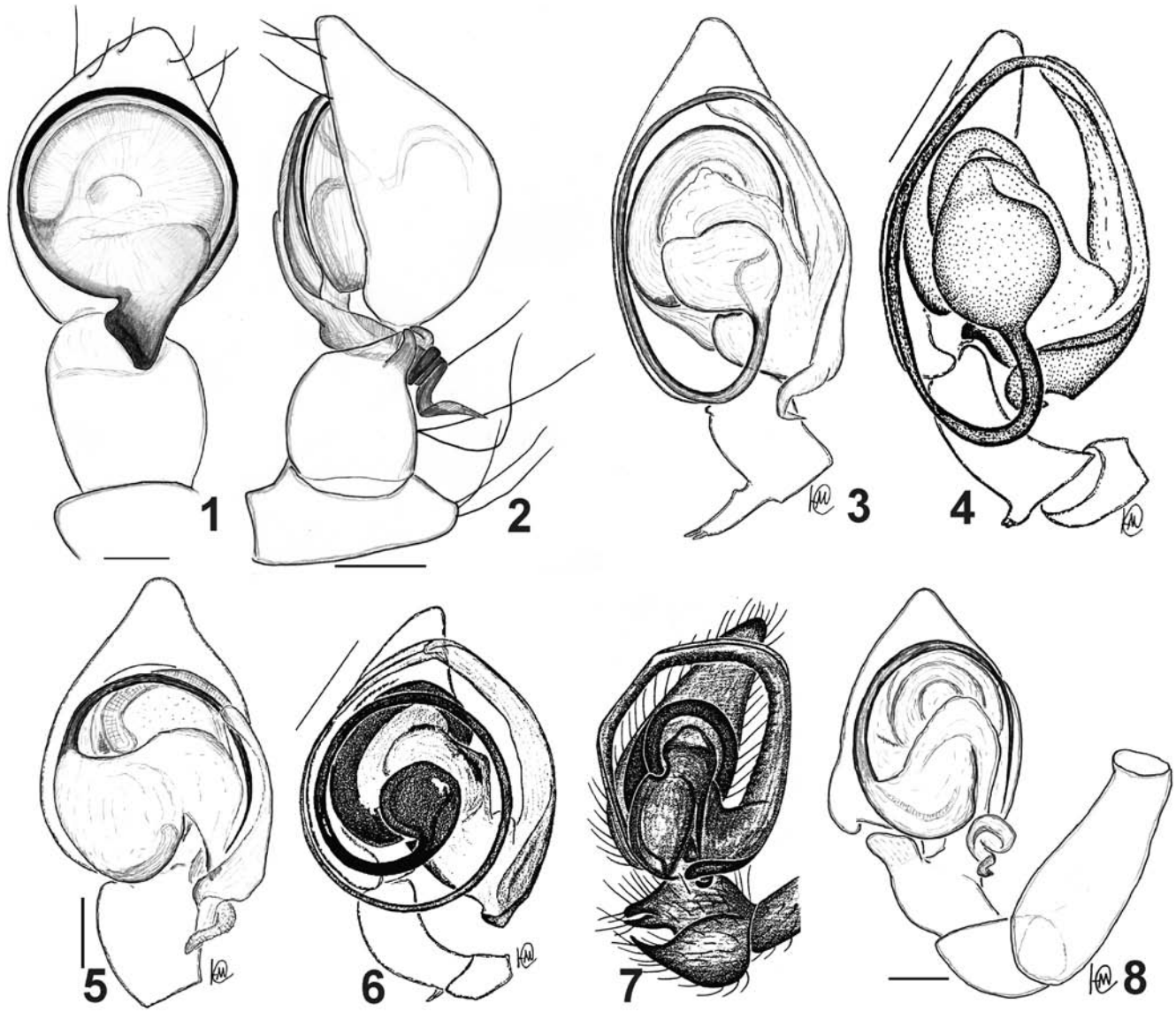
(2) Screwed terminal part can be subdivided into a horizontal portion (*Ch*) and the screw proper (*Cs*) (Figs. 15, 17, 20). The horizontal portion is partly hidden by the lateral tibial apophysis. The first loop of the screw begins in the socket formed by the tibial apophyses, cymbium and tibia. The screw proper can be slightly conical (decreasing in diameter toward the tip), approximately cylindrical, or the terminal part can be wider than the other loops.

(3) Coiled apical portion flat, ribbon-like, forming two coils (*Cl*1 and *Cl*2) lying one above the other (Figs. 15, 17–19). Width of apical portion gradually decreases and terminal part of conductor is sharply pointed (*Ct*). Surface of external coil (*Cl*1) covered with denticles (*Cd*, Fig. 9), inner part of ribbon with radial wrinkles. The outer surface of the ribbon has a groove (Figs. 10, 20: *Cf*) serving as a sheath which holds and guides the embolus. The angle between the apical coils and terminal screw is slightly over 90°.

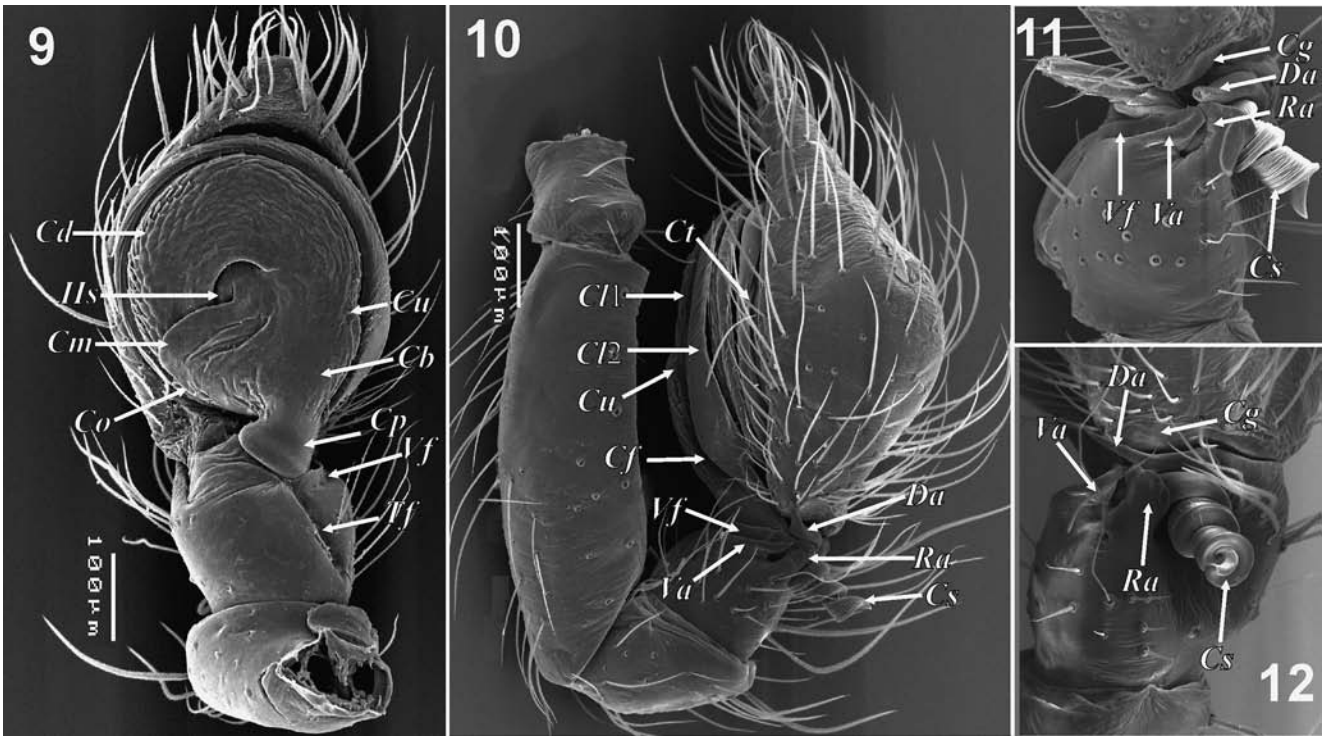
What we refer to as the conductor's pedes was called the conductor by Shear (1967). Earlier, this part was described as a ''triangular plate'' by Gertsch (1946) and Chamberlin & Gertsch (1958). It seems that the apical portion of the conductor was overlooked by earlier authors.

The whole conductor was recently named the ''dictynid tegular apophysis'' by Coddington (1990). We cannot accept this term, because the homologous structure in the Tegenariini (Agelenidae), Cybaeidae and related groups is called the conductor [cf. Gertsch (1946), Lehtinen (1967), Roth & Brame (1972)]. The concept of conductor in this sense was presented already by Comstock (1910: 168).

Embolus (*Em*): Long and coiled, in lateral view it looks whip-shaped (Figs. 13, 15, 17–19). In dorsal view it is ribbon-shaped with a thick cylindrical external part, the embolus proper, and a membranous inner part (*Ee*, Fig. 14). The embolus makes the same number of coils as the conductor. The base of the embolus (*Eb*, Figs. 20–21) can be situated in different parts of the circle in



Figs. 1–8: Left male palps of several species of Dictynidae. **1–2** *Lathys stigmatisata*, ventral and retrolateral views respectively; **3** *Dictyna felis* (lectotype of *Dictyna hummeli* Schenkel, 1936); **4** *Emblyna logunovi*; **5** *Sudesna hedini* (syntype); **6** *Emblyna kaszabi*; **7** *Tivyna moaba* (Ivie, 1947) (after Chamberlin & Gertsch, 1958); **8** *Ajmonia capucina* (syntype). Scale lines=0.1 mm.



Figs. 9–12: Left male palps. **9** *Lathys stigmatisata*, ventral. **10–12** *L. alberta*. **10–11** Retrolateral; **12** Dorso-retrolateral. Abbreviations: *Cb*=base of conductor; *Cd*=denticles of conductor; *Cf*=conductor's furrow; *Cg*=cymbial groove; *Cl*1 and *Cl*2=loop 1 and 2 of apical portion of conductor; *Cm*=membranous part of conductor; *Co*=lobe of conductor; *Cp*=pedes of conductor; *Cs*=screw of conductor; *Ct*=tip of conductor; *Cu*=extension of upper part of pedes; *Da*=dorsal apophysis; *Hs*=apical haematodocha, terminal part; *Ra*=intermediate (dorso–lateral) apophysis; *Tf*=tibial furrow; *Va*=lamellate lateral apophysis; *Vf*=longitudinal furrow of *Va*.

different species. Although the base of the embolus looks rather simple, it is complicated and is coiled around the sclerotised part of the apical haematodocha (*Es*, Fig. 18).

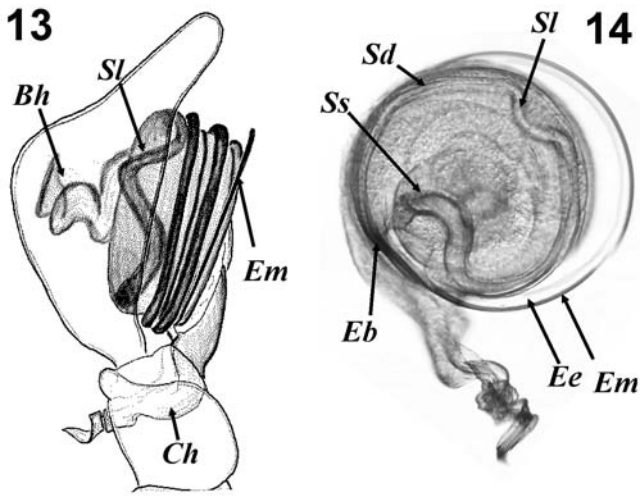
Almost the whole conformation of the bulbus in the *stigmatisata* group is based on screws and coils.

Epigyne and spermathecae

Although the main aim of this paper is to describe the morphology of the male palp, we decided to describe briefly the female epigyne, with special emphasis on those parts of the epigyne which correlate functionally with the male palp. The epigyne is weakly sclerotised, with two openings. The round receptacula, insemination ducts and fertilisation ducts are visible through the partly transparent cuticle.

Epigynal openings: All species of the *stigmatisata* group studied have two separate openings (*Eo*), widely or closely spaced (Figs. 22, 25). An opening can lead directly to an insemination duct or to an atrium of variable size (*Ea*) (Figs. 23–24). The size of the atrium seems to be correlated with the diameter and length of the terminal part of the conductor's screw. The atrium has more or less distinct threading (*At*). The large terminal portion of the conductor in *L. stigmatisata* and *L. spasskyi* Andreeva & Tyshchenko, 1969 corresponds to wide openings and a deep atrium (Figs. 24–25). In *L. alberta* Gertsch, 1946 (Fig. 22) and *L. maculosa* (Karsch, 1879), which have small terminal parts to their conductors, the female epigynes have small openings and atria which are almost or totally absent.

Insemination ducts: The insemination ducts are very long, and they form two groups of coils: apical (*Ia*) and basal (*Ib*) (Figs. 23–24). The apical coils are situated below the openings and lie horizontally (parallel to the epigastric furrow). The basal coils are wrapped over the receptacula (*Re*) and fertilisation ducts (*Fd*), and are vertical (at right angles to the apical coils) or oblique. The number of vertical and horizontal coils ranges from one to three in different species. The receptacula have a distinct, rather large pore (*Rp*) (Fig. 23).



Figs. 13–14: Left male palps. **13** *Lathys alberta*, prolateral; **14** *L. spasskyi*, tegulum, dorsal. Abbreviations: *Bh*=basal haematodocha; *Ch*=horizontal portion of conductor; *Eb*=base of embolus; *Ee*=membranous part of embolus; *Em*=embolus; *Sd*=seminal duct; *Sl*=seminal duct loop; *Ss*=origin of *Sd*.

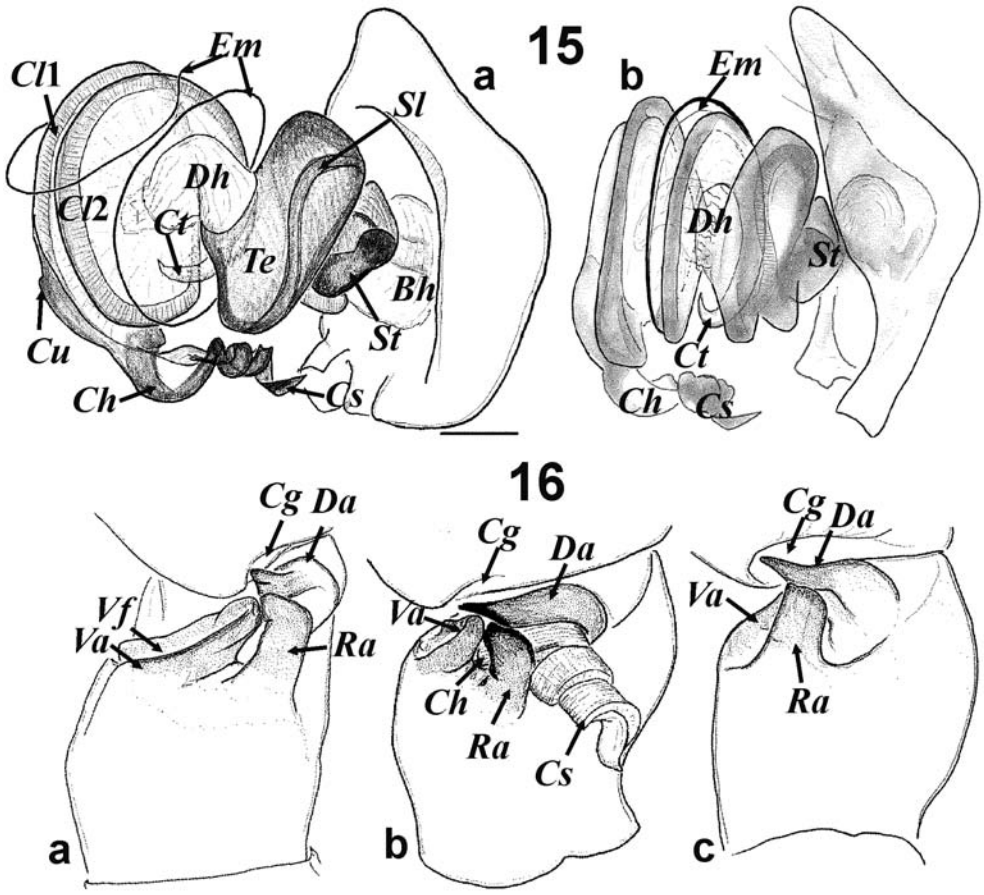
It appears that the number and size of coils corresponds to the length of the embolus and the apical portion of the conductor. Often epigynes contained a broken embolus in their insemination ducts. In all of the observed cases males left a broken embolus in both halves of the epigyne. An instance of a lost embolus in *Lathys* was described by Wiehle (1967); however, we never saw an embolus penetrating the receptacula as illustrated by Wiehle (1967).

Unique features of the genitalia in the *L. stigmatisata* group

Clamped conductor: We do not know of any similar case where the conductor is totally clamped in position by the tibial apophyses. Although several *Dictyna* species [*D. arundinacea* (Linnaeus, 1758), *D. pusilla* Thorell, 1856, *D. alaskae* Chamberlin & Ivie, 1947, etc.] have conductors with screwed terminal parts, they have no tibial apophyses. Although members of the Cicurininae have tibial apophyses, their conductors are never screw-shaped. It seems that *Lathys* species from the other species groups do not have the tip of their conductor clamped, for example *L. foxi* (Marx, 1891) and *L. pallida* (Marx, 1891) (see Paquin & Dupérré, 2003).

Coiled ribbon-shaped apical arm of conductor: Although many members of the Dictyninae, Cybaeidae and *Malthonica* (Agelenidae) have a two-armed conductor with a flat apical portion, their conductor never forms coils. Judging from the figures, the conductor of *Tosyna calcarata* (Banks, 1904) (Dictyninae) (cf. Chamberlin & Gertsch, 1958: fig. 17.1) makes almost one coil. Nevertheless, none of the dictynids, or members of other families has a conductor with ribbon coils lying one over another.

Coiled-screwed architecture: There are rather many dictynids with screwed conductor tips, for example *Mallos niveus* O. P.-Cambridge, 1902 (Chamberlin & Gertsch, 1958: plate 8, figs. 7–8), *M. gregalis* (Simon, 1909), *Tricholathys spiralis* Chamberlin & Ivie, 1935, *Arctella lapponica* Holm, 1945, *Phantyna varyna* Chamberlin & Gertsch, 1958, *P. rita* Gertsch, 1946, *Dictyna bellans* Chamberlin, 1919, *D. arundinacea*, *D. alaskae*, *D. pusilla*, *Sudesna hedini* (Schenkel, 1936) (Fig. 5), *Ajmonia capucina* (Schenkel, 1936) (Fig. 8) and many others. However, none of these species has a coiled embolus or apical arm of the conductor. On the other hand, the few species with a long apical portion of their conductor forming almost one complete coil, e.g. *Tivyna pallida* (Keyserling, 1887) or *T. moaba* (Ivie, 1947) (Fig. 7), have



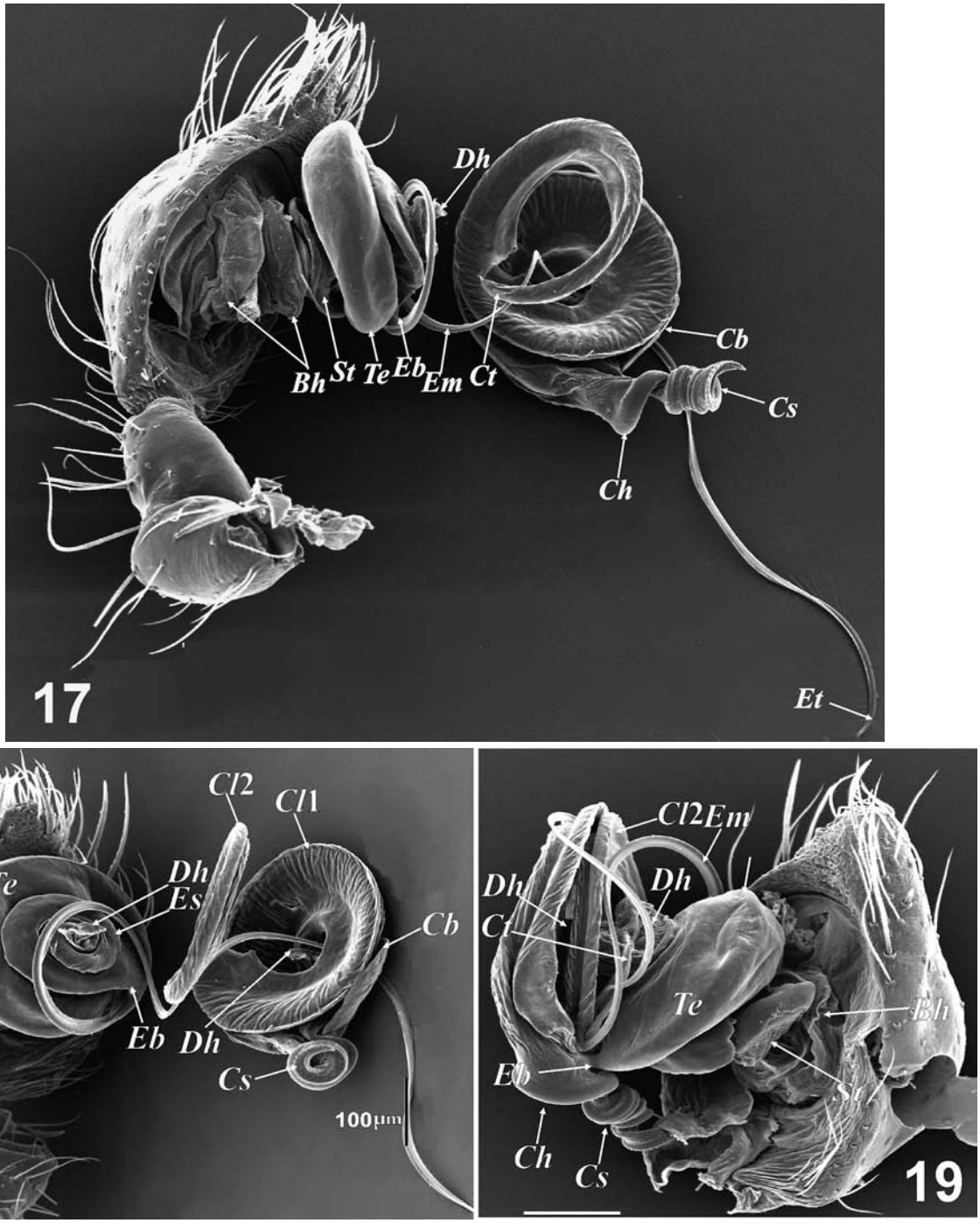
Figs. 15–16: Expanded left palp of *Lathys alberta*, retrolateral (**15**), and palpal tibia (**16**). **15a** Strongly expanded bulbus; **15b** Slightly expanded bulbus; **16a–c** Retrolateral, dorso-retrolateral and dorsal views, respectively. Abbreviations: *Bh*=basal haematodocha; *Cg*=cymbial groove; *Ch*=horizontal portion of conductor; *Cl*1 and *Cl*2=loop 1 and 2 of apical portion of conductor; *Cs*=screw of conductor; *Ct*=tip of conductor; *Cu*= extension of upper part of pedes; *Da*=dorsal apophysis; *Dh*="apical" haematodocha; *Em*=embolus; *Ra*=intermediate (dorso–lateral) apophysis; *Sl*=seminal duct loop; *St*=subtegulum; *Te*=tegulum; *Va*=lamellate lateral apophysis; *Vf*=longitudinal furrow of *Va*. Scale line=0.1 mm.

a very short terminal part. Several East Palaearctic species with a long embolus have a short apical portion of their conductor (see Figs. 3, 4, 6). The single species with a long and coiled embolus, *''Emblyna'' kaszabi* Marusik & Koponen, 1998 (Fig. 6), has the coils placed in one plane, and its conductor has no screwed or coiled parts.

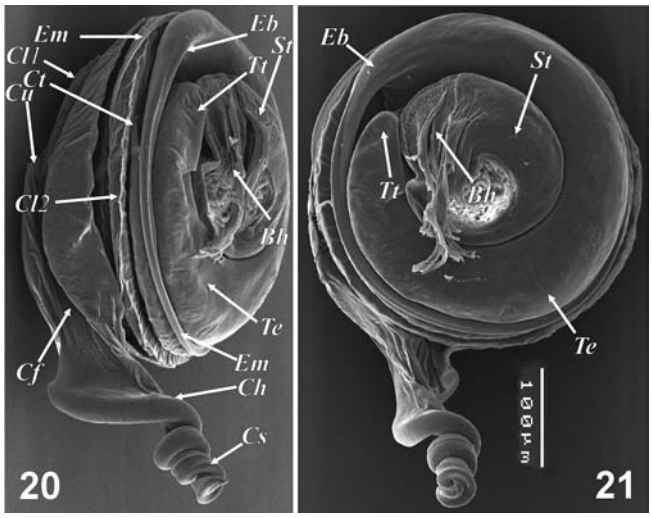
In the *L. stigmatisata* group all parts of the bulbus, including the base of the embolus, are coiled.

Base of embolus: Hidden by conductor in ventral view, and has no fixed position (cf. Dictyninae where it is situated at 6–10 o'clock on left palp). It is situated on the prolateral side of the tegulum in almost all Amaurobioidea (Agelenidae, Amaurobiidae, Gnaphosidae, Lycosidae). An exception is the Hahniidae, where the embolus originates on the retrolateral side of the tegulum.

Lost embolus: Another unusual feature of the *L. stigmatisata* group is the breaking off of the male embolus during mating. We do not know if males always lose a part of their embolus in the female's insemination duct, or only occasionally. The breaking off of the embolus during mating is well known in the theridiid genus *Latrodectus*. Unlike *Latrodectus*, the embolus in *Lathys* has no breaking point. We do not know of any



Figs. 17–19: Expanded left palp of *Lathys alberta*. **17, 18** Prolateral; **19** Retrolateral. Abbreviations: *Bh*=basal haematodocha; *Cb*=base of conductor; *Ch*=horizontal portion of conductor; *Cl*1 and *Cl*2=loop 1 and 2 of apical portion of conductor; *Cs*=screw of conductor; *Dh*=''apical'' haematodocha; *Eb*=base of embolus; *Em*=embolus; *Es*=coiled sclerotised part of base of embolus; *Et*=embolic tip; *St*=subtegulum; *Te*=tegulum.



Figs. 20–21: Left bulbus of *Lathys alberta*. **20** Retrolateral; **21** Dorsal. Abbreviations: *Bh*=basal haematodocha; *Ch*=horizontal portion of conductor; *Cl*1 and *Cl*2=loop 1 and 2 of apical portion of conductor; *Cs*=screw of conductor; *Cu*=extension of upper part of pedes; *Eb*=base of embolus; *Em*=embolus; *St*=subtegulum; *Te*=tegulum; *Tt*=tip of tegulum.

other case in the Dictynidae, or in the related Agelenidae, Hahniidae and Amaurobiidae, where the embolus may be left in the epigyne.

Three tibial apophyses: Most Dictyninae have no real tibial apophyses, with the exception of some Nearctic species, of which several are uncertainly placed, such as *"Dictyna" quadrispinosa* Emerton, 1919, *Tivyna moaba* and *Phantyna micro* (Chamberlin & Ivie, 1944). These species have several tibial apophyses. Members of the Cicurininae always have more than one apophysis, situated on the retrolateral side. Probably only members of the *L. stigmatisata* group and possibly a few other *Lathys* species have a dorsal tibial apophysis.

Epigyne: The epigyne of *Lathys* is unusual among the Amaurobioidea in having long insemination ducts. Similar ducts are present only in a few taxa, such as in the Hahniidae, *Cicurina*, *Brommella*, and some Tegenariini (*Azerithonica*).

Some speculations about mating behaviour

It appears that all *Lathys* species copulate in a rather unusual way. Judging from the conformation of the male palp and epigyne, males orient the dorsal (cymbial) side of their palp to the epigyne. Then, when the screw penetrates the atrium, the male possibly slightly rotates the palp to achieve deeper penetration of the atrium.

As the conductor cannot rotate, it seems that only the rotation of the tegulum pushes the embolus into the long coiled insemination duct. During haematodochal expansion the plane of the conductor turns perpendicular to the axis of the tibia. At the same time, the part of the conductor bearing the tip of the embolus approaches the lateral tibial apophysis. It appears that the furrow on the lateral tibial apophysis (*Vf*) serves as an extension of the conductor's furrow (*Cf*), and both furrows serve as a guide for the embolus.

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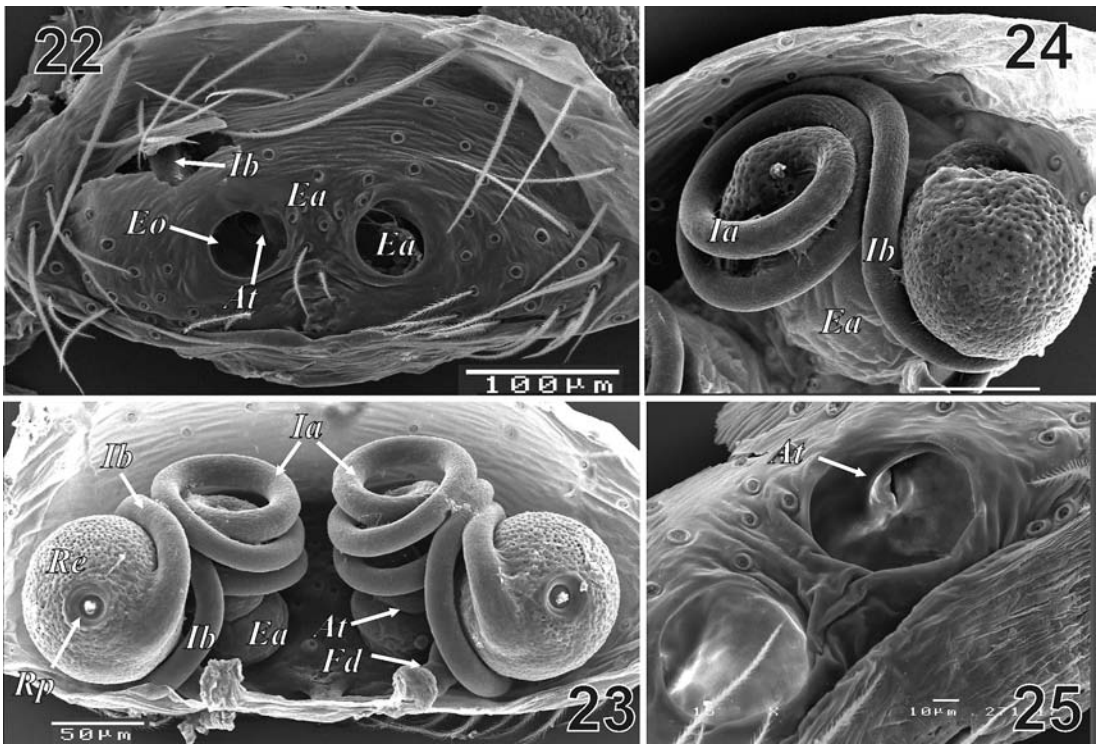

Figs. 22–25: Epigynes. **22–23** *Lathys alberta*. **22** Ventral; **23** Dorsal. **24–25** *L. spasskyi*. **24** Dorsal; **25** Ventral. Abbreviations: *At*=threading of atrium; *Ea*=epigynal atrium; *Eo*=epigyne opening; *Fd*=fertilisation duct; *Ia*=apical portion of insemination duct; *Ib*=basal portion of insemination duct; *Re*=receptaculum; *Rp*=pore of receptaculum.

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