

Erection of infrageneric groupings within the spider genus *Clubiona* Latreille, 1804 (Aranei Clubionidae): a typological approach

Выделение внутриродовых группировок в роде пауков *Clubiona* Latreille, 1804 (Aranei Clubionidae): типологический подход

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КЛЮЧЕВЫЕ СЛОВА: типология, морфология, внутривидовые группировки, *Clubiona*.

ABSTRACT: By means of a newly rediscovered typological approach in the spider genus *Clubiona*, here restricted solely to the scope of the Holarctic fauna, four subgenera are established, with 15 species groups and 10 species subgroups distinguished in the subgenus *Clubiona* s.str. alone. A thorough analysis of all morphological diagnostic characters of the species representing various species subgroups, groups, and subgenera is provided. The subgenera are based on three main and one combined morphological type, with mostly conjugated characters of male and female genitalia underlying each infrageneric grouping.

РЕЗЮМЕ: При помощи типологического метода в составе рода *Clubiona* (в объеме голарктической фауны) выделено 4 подрода, а в подрode *Clubiona* s.str. 15 групп и 10 подгрупп видов. Охарактеризованы 3 основных и один комбинативный морфотип *Clubiona*, на основании которых выделены подроды. Основой для выделения всех указанных группировок являются признаки гениталий самцов и самок, в большинстве случаев сопряженные. Обсуждается уровень морфологической генеральности признаков и сходства видов, включаемых в различные внутриродовые группировки *Clubiona*. Даны диагнозы и краткие описания всех выделенных группировок, охарактеризован их видовой состав.

Introduction

The present contribution can be considered as an attempt to apply the recently formalized typological procedure [Meyen, 1978; Lyubarsky, 1991] to spider systematics. Typology is considered here as a well-grounded discipline without any insulting sense sometimes applied to this term [e.g. Mayr, 1963: 5, 16-17; 1968: 24-25, 66-68].

To sum up, modern typology can be briefly outlined as a discipline operating with the terms archetype, meron, and taxon. Meron is a regular, homologized, naturally distinguishable character. As a pattern of meron change, archetype is not a particular organization structure, being only an

image, a term enriched by characters sometimes excluding each other within a single organism. An archetype consists of merons as the entire of units. From a logical viewpoint, taxon corresponds to the volume, and archetype to the contents, of a term.

The main typological procedure lies in an iterated process of classification (taxon after taxon) and division (meron after meron) as well as in allotting the taxon a rank.

There is no direct relation between meronomic and taxonomic hierarchies. In contrast, a meronomic-taxonomic discrepancy (non-correspondence, by the original definition — Lyubarsky, 1991) is observed in most cases. Moreover, taxa and merons cannot be treated as unambiguously corresponding to each other. Having fixed a meron, we get a number of taxa of various ranks displaying this meron. A meronomic-taxonomic relation is an extreme case of such a meronomic-taxonomic incongruence, this being true when all constituents within a group are distinguishable by characters of the same kind. In other words, the taxa differing by the mode of a single character are of the same rank.

One of the most important criteria of a taxonomic rank in typology is the level of generalism of the deciding, most strongly modified, distinguishing meron (diagnostic character).

Typology offers no new methods in systematics, it only lays a logical foundation for the traditional techniques of morphology.

In particular, typology is used below for the separation of infrageneric groupings routinely treated as quite obscure complexes often supplied by indistinct diagnoses and displaying vague limits. Such groupings have been distinguished within *Clubiona* in the scope of both European and North American faunas [Lohmander, 1945; Wiehle, 1965; Dondale & Redner, 1982]. Our own data concerning the entire Holarctic fauna mainly confirm the groupings established earlier, with the addition of several new ones recently described in the Oriental realm [Mikhailov, 1990, 1991, 1994]. At present all those groupings have become accepted in the arachnological literature [e.g. Ono, 1992; Hayashi & Yoshida, 1993], yet the grounds for the separation

of the infrageneric groupings in *Clubiona* have never been discussed in due detail [cf. Mikhailov, 1992a, 1995].

The first part of this study puts forth typological arguments, with some inevitable repetitions implied by the method of successive approximation (or reciprocal illumination — cf. Hennig, 1979: 21-22).

Material

Pertinent material serving the basis for this work comprises 71 *Clubiona* species of the ex-USSR list [cf. Mikhailov, 1992b], representing all 15 species-groups of the Holarctic fauna. In addition, high quality (re)descriptions and illustrations [e.g. Edwards, 1958; Wiehle, 1965; Dondale & Redner, 1982, etc.] have allowed to consider further seven species from West and Central Europe, 40 Nearctic species as well as some (not all) *Clubiona* forms deriving from Japan, Korea, and China.

The following abbreviations are accepted below: CO — copulatory openings, CT — copulatory tubes, E — embolus, EB — embolar base, EP — embolar part, SPT(ae) — spermatheca(e), TiA — apophysis of palp tibia, TP — tegular part.

Methods

The basic method of typology, be it applied to biology or any other science, lies in establishing some essential similarities (= homologies) and comparing the subjects by separate similarities. Traditionally, i.e. according to typology sensu lato, such characters as the structure and conformation of the male and female genitalia have been used both for the construction of an infrageneric classification and the separation of species of the genus *Clubiona*.

Other features examined (measurements of body and leg articles, leg armature, width of eye area, coloration) are either of no taxonomic value or are important solely at the generic level. Thus, leg armature and reciprocal ratios of leg articles provide a safe recognition of the genera *Clubiona*, *Elaver*, and *Cheiracanthium*. In some cases, the pattern of dorsal abdominal coloration promotes species identification, e.g. *C. japonica*, *C. jucunda*, *C. riparia*, *C. subsultans*. Yet the latter character is unstable, being significant only in several species out of over 80 considered here.

Below, both minimal and maximal levels of morphological generalism of *Clubiona* are taken as purely axiomatic, i.e. without further discussion. Minimally, species differs by certain features of genital structure and maximally, there are some

generic non-sexual differences. A *Clubiona*-like structure of the genitalia is found in Gnaphosidae, whereas *Cheiracanthium* displays quite a different pattern. The latter genus seems to be closer either to Sparassidae (Lehtinen, personal communication) or to Miturgidae (N. Platnick, personal communication). The problem of the upper taxonomical limit of the groupings established below in *Clubiona* is also left without comment. Some of them possibly represent true genera, as it was tentatively suggested by Lohmander [1945].

It is shown below the specific meronomic-taxonomical relation [Lyubarsky, 1991] can be applied to the infrageneric groupings of *Clubiona*, and the characters of genital structure considered at various levels of generalism correspond directly to the infrageneric taxa.

Being the most strongly modified compared to other organs at the species level, both deviation extent and stability enjoy a causal explanation from a viewpoint of the biospecies concept. Evolution of the Order Aranei is generally considered to be associated with the development of spinning activity¹ against the background of a considerably uniform morphology in the traditional sense.

Differences in the structure of the copulatory organs are highly important as ensuring a profound species reproductive isolation.

A more detailed consideration of the male genitalia of *Clubiona* is given further.

In each male spider, the main part of the palpus², namely bulb (bulbus), is subdivided both morphologically and functionally into the following merons: subtegular part, TP, and EP (Fig. 1), all of obscure origin (for different hypotheses, see Ivanov, 1965: 154; Kraus, 1984; Coddington, 1990; four parts are distinguished by Shear, 1981). Among *Clubiona* species, TP varies greatly by the extent of sclerotization. It seems more likely we deal with secondary membranization of TP, which is very characteristic of the family Clubionidae and some closely related groupings [Kraus, 1984].

Main considerations

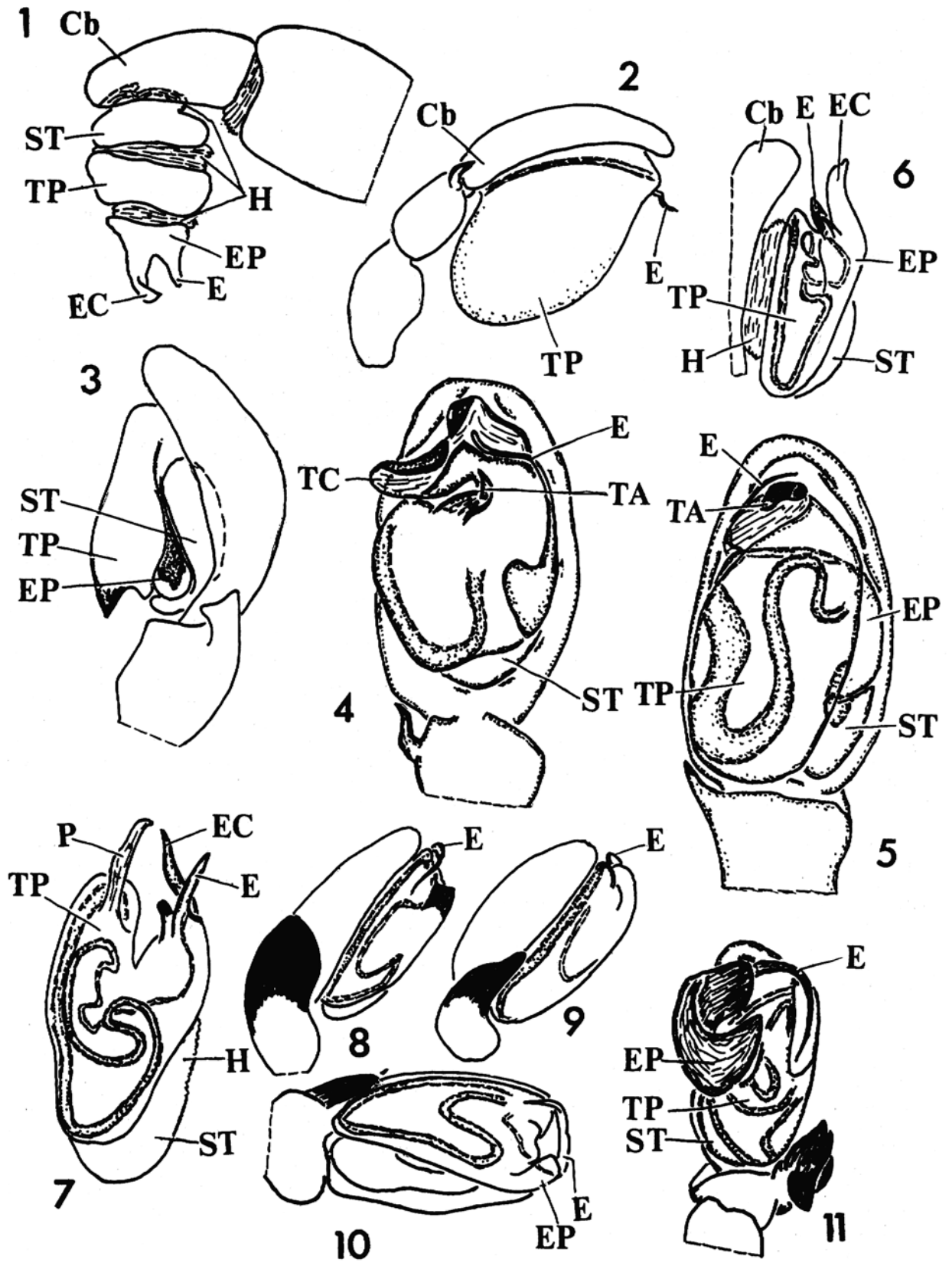
Analysis can be started from the following point. Let a grouping with a completely membranized TP

¹ As stated by Lange [1969: 56], this term is more preferable than the earlier "web industry".

² Palpus is treated here as the part of a male palp which functionally participates in copulation.

Figs 1-11. Structure of male palp in the genus *Clubiona*: 1 — hypothetical primitive construction, 2-11 — morphological types: 2-3 — *Paraclubiona*: *C. corticalis*, 3 — *C. kurosawai*, 4 — *Japoniona*: *C. japonica*, 5 — *Bicluona*: *C. jucunda*, 6-11 — *Clubiona* s.str.: 6 — *C. marmorata*, 7 — *C. reclusa*, 8 — *C. trivialis*, 9 — *C. subtilis*, 10 — *C. basarukini*, 11 — *C. abboti*. 1-3, 6, 8, 9 — lateral view, 4, 5, 10, 11 — ventral view, 7 — bulb, ventrally. 1 — after Kraus, 1984, 2, 6, 9 — after Wiehle, 1965, 3 — after Ono, 1986a, 11 — after Dondale & Redner, 1982. Abbreviations: Cb — cymbium, E — embolus, EC — conductor of embolar type, EP — embolar part, H — hematodocha, P — protector, ST — subtegulum, TA — tegular apophysis, TC — conductor of tegular type, TP — tegular part.

Рис. 1-11. Строение пальпы самца в роде *Clubiona*: 1 — гипотетическая примитивная конструкция, 2-11 — морфологические типы: 2-3 — *Paraclubiona*: *C. corticalis*, 3 — *C. kurosawai*, 4 — *Japoniona*: *C. japonica*, 5 — *Bicluona*: *C. jucunda*, 6-11 — *Clubiona* s.str.: 6 — *C. marmorata*, 7 — *C. reclusa*, 8 — *C. trivialis*, 9 — *C. subtilis*, 10 — *C. basarukini*, 11 — *C. abboti*. 1-3, 6, 8, 9 — вид сбоку, 4, 5, 10, 11 — вентрально, 7 — бульбус, вентрально. 1 — по: Краус, 1984, 2, 6, 9 — по: Wiehle, 1965, 3 — по: Оно, 1986а, 11 — по: Dondale & Redner, 1982. Сокращения: Сб — цимбиум, Е — эмболюс, ЕС — кондуктор эмболярного типа, EP — эмболярный отдел, H — гематоодоха, P — протектор, ST — субтегулум, TA — вырост тегулула, TC — кондуктор тегулярного типа, TP — тегулярный отдел.



(1) include the species with EP either sclerotized (1a) or non-sclerotized (1b; Fig. 2). A considerable enlargement of TP is peculiar in the latter case. In another grouping (2), TP sclerotization is expressed only fragmentarily, being provided by a hook- or hammer-like outgrowth (Figs 4-5); EP is sclerotized insignificantly and TP enlargement is absent.

Beyond these groupings, there are some species with both TP enlargement and a non-sclerotized EP, combined with a fragmentarily sclerotized TP (1', Fig. 3). It is remarkable that the sequence of splitting into groupings firstly by TP (1-2) and then by EP (1a-1b) accepted here is quite arbitrary and can be changed into the reverse mode.

Species with strongly sclerotized EP (1a) differ by peculiarities of both E and EP-apophysis (Figs 6-7, 11, etc.). Apparently, these details represent less generalized characters than sclerotization-membranization of either both totally TP & EP or TP-enlargement. A considerable bulb-enlargement of some species of this grouping (*C. genevensis*, *C. viridula*, etc.) is due to EP, mainly to E itself.

As a rule, TiA is well-developed and is important for species determination in grouping 1a (Figs 8-10 etc), whereas in other *Clubiona* it is either weakly-developed (1b + 1') or rather uniform, although it can be used for species identification as well (2).

E is functionally associated with a certain structure of either tegular or embolar nature, known as conductor. In some species, the function of the conductor in copulation is obvious, lying in directing the embolus movement. Such a conductor with a well-expressed role is common in the following groupings: most species of 2 (of tegular nature), two representatives of 1b + 1' (*C. pyrifera*, *C. kurosawai*, also of tegular nature), and certain species of 1a (of embolar nature — Figs 6, 7). The conductor in grouping 2 is weakly sclerotized, but it is peculiar in shape, surrounding E from three sides except ventrally (Fig. 4). In many species, a long and thin E of the slipping-type (after Wiehle, 1965: Einstoß-Embolus) lies calmly, i.e. in a non-erected position, on the tegular surface (see Figs 23, 25, 59, 62, etc.). That extent of TP surface is distinguished by strong membranization, it has been named earlier also a "conductor", whereas its function remains obscure. A membranous outgrowth of TP in *C. reclusa* and related species is known as protector [Wiehle, 1965]. It arises at the tegular apex in the same place as does the "conductor" of other species (Fig. 6). A less strongly expressed "protector" supporting the calm position of a thick and long E is characteristic of the *C. lutescens*-group ("P" in Fig. 27). Significance of all these membranous outgrowths is also obscure.

Therefore, the main morphological types of the male copulatory organs can be described as follows:

Morphotype 1b + 1'. TP strongly enlarged, rarely sclerotized in part. TiA weakly developed. Rarely membranous conductor of tegular type.

Morphotype 2. Tegulum developed normally, partly sclerotized as an outgrowth peculiar in shape. TiA developed, of specific shape. Conductor (lacking in *C. jucunda*) of tegular type and specific in shape, more strongly sclerotized than in the previous morphotype.

Morphotype 1a. Tegulum normal, non-sclerotized. TiA varies from very weakly to very strongly developed. Conductor, if any, of embolar type. Sometimes membranous protector/"conductor" structures on tegulum.

The necessity in merging 1b and 1' groupings is confirmed below by the data obtained upon the female genitalia.

How well do the above male morphotypes correspond to the female ones? Surprisingly, an almost equal arrangement of the groupings is found in female *Clubiona* as well.

Similarly to other spiders, the *Clubiona* endegyne, i.e. the inner female genitalia, opens by paired CO of different shape ranging from circular to fissure-like. Sometimes CO open into a single midline groove. CO are disposed at the fore (type 1b + 1', Fig. 12), middle (type 2, Fig. 13), and hind (type 1a, Figs 14-22 etc.) part of the genital plate. Beginning from CO, paired CT direct backwards (1b + 1'), forwards (1a), or straight toward the depth of the endegyne (2). The only exception is *C. jucunda*, representing a species with the male and female attributed to different morphotypes, 2 (Fig. 5) and 1a (Fig. 14), respectively. This species belongs to a mixed morphotype [Mikhailov, 1994].

Hence, the diagnoses of the morphotypes given above (except of *C. jucunda*) must be complemented as follows:

1b + 1'. CO in the fore part of the epigyne. CT directed backwards.

2. CO at the middle part of the epigyne. CT directed straight into the depth of the endegyne.

1a. CO in the hind part or at the hind edge of the epigyne. CT directed strongly forwards.

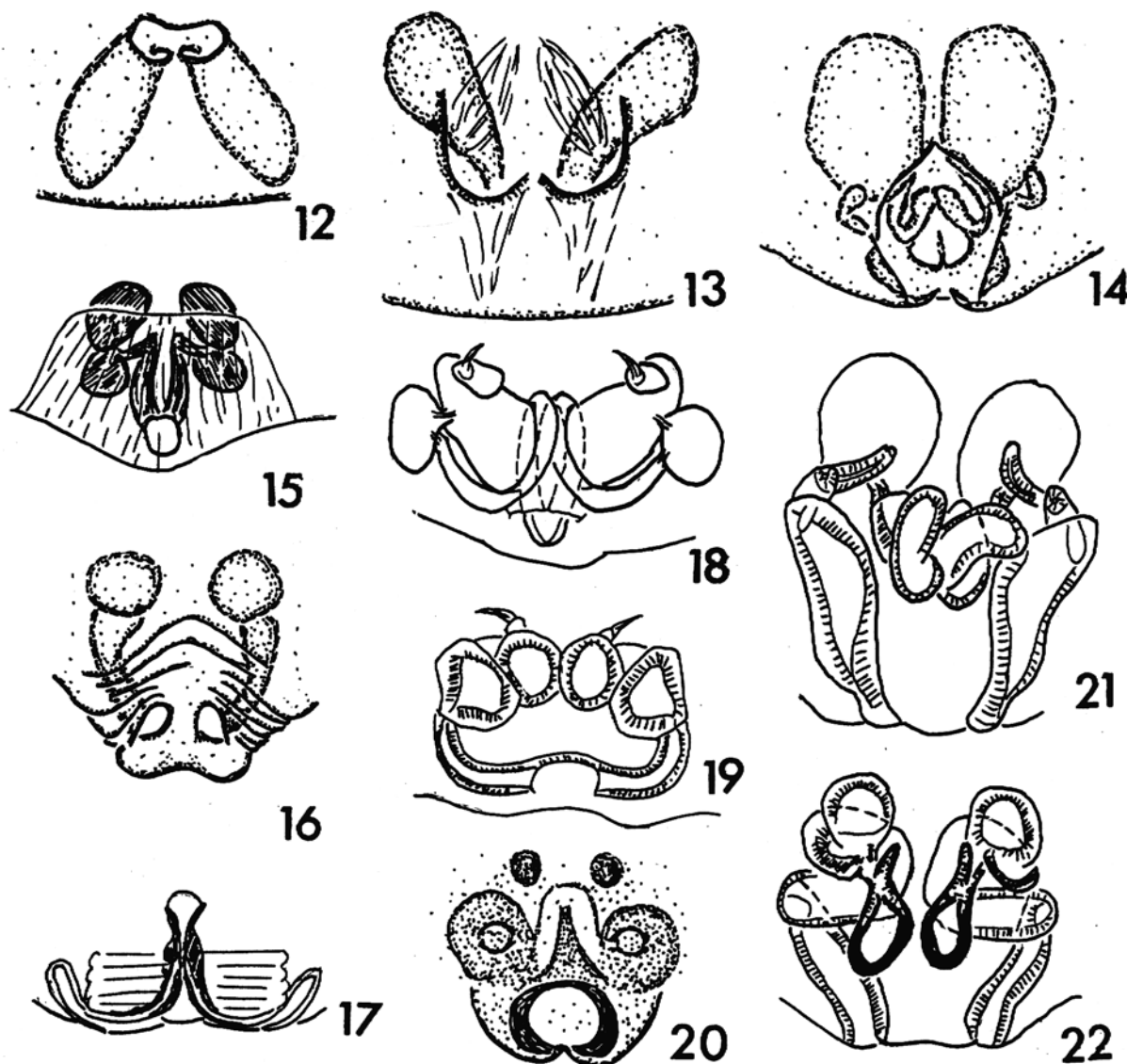
Each of these morphotypes is here allotted the subgeneric status. The basic differences between *Clubiona* subgenera lie in the structure of the bulb and the direction of the epigynal tubes, both apparently more general characters. On the other hand, at the species level such details as the structure of TP, EP, and TiA, as well as SPTae and atria are more valuable. According to the principle of the specific meronomic-taxonomical relation, these latter five characters are obviously less generalized than those of the subgenera.

C. jucunda deserves separation into a fourth subgenus.

As a result, in the scope of the entire Holarctic fauna³, the following *Clubiona* subgenera are to be distinguished: *Paraclubiona* (Lohmander, 1945)⁴ — ca. 30 species of morphotype 1b + 1' in Europe, Caucasus, E-Asia with China, Himalaya, presumably also in Australia and SE-Asia; *Japoniona* Mikhailov, 1990 — morphotype 2, 3 species from E-Asia; *Bicluona* Mikhailov, 1994 (single species, E-Asia), and *Clubiona* s.str. — morphotype 1a, distributed worldwide, perhaps except S-America, comprising the bulk of species diversity of the genus (about 350).

³ With some additions from the world fauna.

⁴ Earlier [Mikhailov, 1990: 143] when applying a subgeneric status to *Paraclubiona*, it was erroneously indicated "comb.n.". Actually, for the first time this status had been established by Tullgren [1946].



Figs 12-22. Structure of female epigyne and vulva in the genus *Clubiona*: 12 — *Paraclubiona*: *C. corticalis*, 13 — *Japoniona*: *C. japonica*, 14 — *Bicluona*: *C. jucunda*, 15-22 — *Clubiona* s.str.: 15 — *C. trivialis*, 16 — *C. abboti*, 17 — *C. maritima*, 18 — *C. brevipes*, 19 — *C. comita*, 20 — *C. genevensis*, 21 — *C. terrestris*, 22 — *C. similis*. 12-15 — epigyne, 16-19 — vulva, ventrally, 21-22 — vulva, inner view (dorsally). 12, 18-22 — after Wiehle, 1965, 15, 17 — after Dondale & Redner, 1982.

Рис. 12-22. Строение эпигины и вульвы самки в роде *Clubiona*: 12 — *Paraclubiona*: *C. corticalis*, 13 — *Japoniona*: *C. japonica*, 14 — *Bicluona*: *C. jucunda*, 15-22 — *Clubiona* s.str.: 15 — *C. trivialis*, 16 — *C. abboti*, 17 — *C. maritima*, 18 — *C. brevipes*, 19 — *C. comita*, 20 — *C. genevensis*, 21 — *C. terrestris*, 22 — *C. similis*. 12-15 — эпигина, 16-19 — вульва, вентрально, 21-22 — вульва, вид изнутри (дорсально). 12, 18-22 — по: Wiehle, 1965, 15, 17 — по: Dondale & Redner, 1982.

Besides the subgeneric level, certain structural peculiarities of the male (EP and TP) and female (CO, CT, atria, SPTae) allow to separate groupings of yet another, lower, level traditionally allotted in arachnology the rank of species-groups, this time of no nomenclatorial status. Such an extra-nomenclatorial status of species-groups is highly convenient for practical taxonomy, reducing the constraints of static nomenclature fixed by the current Code [1985]. Species-groups are in part considered by the Code as *interpolated names* of species complexes [article 6b]. Having no specified names, such groups are cited after the name of the first, by the time of description, species included.

An important basis of species-groups detachment is a conjugation of characters, i.e. an equal volume

of the groupings separately established by male and female genitalic features. In *Clubiona*, such a conjugation appears to be quite unequal to the stereospecificity of the genitalia [Barrientos, 1983]. In several spider taxa, for example, *Micaria* (Gnaphosidae), there is no conjugation, the species-groups being considered as artificial formations for a more simple handling of such species-rich genera. The level of morphological generalism of diagnostic characters of *Clubiona* species-groups is naturally lower than that of the subgenera and higher than that of species. Being functionally stabilized, the characters of genitalia are extremely poorly variable intraspecifically, i.e. lower than at the species level. Intraspecifically, i.e. between species within species-groups, they vary much more considerably.

Table. Polythetic characters of the structure of the male copulatory organs in the *pallidula*-group.
Таблица. Политетические признаки строения копулятивных органов самца в группе *pallidula*.

character/species	<i>sopaikensis</i>	<i>odesanensis</i>	<i>hummeli</i>	<i>ezoensis</i>	<i>pallidula</i>	<i>phragmitis</i>	<i>propinqua</i> -group
thick non-depressed TA	+	+	-	-	-	-	-
thick TA with depressions	-	-	+	+	+	-	-
TA with characteristic bifurcation	-	-	-	-	-	-	+
TA with simple bifurcation	-	-	-	-	-	+	-
E with double crest	-	+	+	-	-	-	-
short E	+	-	-	+	+	+	+

The subgenus *Paraclubiona* includes only one species-group, which formally can be named the *corticalis*-group⁵. This statement is quite preliminary, since numerous species from Southeast Asia and Australia require a modern revision.

Japoniona comprises one group, whereas *Bicluna* is represented by a single species only.

By the conjugation criterion, the following groups are distinguishable within *Clubiona* s.str.:

the *reclusa*-group: a harpoon-like TiA (Figs 60-61) and a typical protector on the male bulb (Fig. 7), a considerable distance between the atrium and SPT, as well as both direction and shape of the tubes and cavities of the female vulva (Figs 49-50);

the *caerulescens*-group: a strong deviation in epigynal structure followed by the male E and TiA (Figs 51, 62; see also Wiehle, 1965, Abb. 106-109));

the *trivialis*-group: a flat TiA combined with a wide E; a simple structure of a circular SPT (Figs 8-10, 15);

the *lutescens*-group: a bifurcate flat TiA combined with a wide E (Figs 27-28); an ovoid atrium combined with a curved tubular SPT (Fig. 21);

the *similis*-group: a bifurcate flat TiA of a different pattern combined with a thin E (Fig. 29); a simple tubular or ovoid non-curved SPT (Fig. 22);

the *abboti*-group: a strongly developed apophysis of EP ("tegular apophysis", after Dondale & Redner, 1982), convex ventro-prolaterally and concave dorso-retrolaterally, combined with a bifurcate, non-flat TiA (Fig. 11); CO paired or fused in a groove, a semicircular CT combined with a wrinkled genital plate projecting beyond the epigastric furrow (Fig. 16);

the *maritima*-group: a big, spur-like EP-apophy-

sis ("tegular apophysis", after Dondale & Redner, 1982) (Fig. 23), slit-like CO combined with a semicircular CT approximating each other, SPTae adjoining each other, and a strongly sclerotized posterior edge of the epigyne (Fig. 17);

the *chabarovi*-group: stereospecificity of a characteristic TiA and the epigynal depressions disposed separately from CO (Figs 52, 63).

With certain reservations, the *obesa*-group (Figs 32-37, 40-47) is also submitted to this criterion, but the conjugated characters of both male and female genitalia display a considerable "infragroup" variability. For example, a broad TiA convex ventrally and concave dorsally is peculiar in the males, but this apophysis can be either turned around the longitudinal axis, as in the *akagiensis*-group, or curved spirally, as in *C. kimyongkii* (Fig. 36). Sinuous CT of the female are typical (Figs 40-42, 44-47), but in the *sapporensis*-subgroup they are almost straight (Fig. 43).

The *pallidula*-group (Figs 48, 53-59) occupies a special position among the others, being distinguished mainly by the structure of the epigyne, namely by the distinctly bifurcate, tubular, rarely ovoid SPTae, as in Fig. 48. The males are characterized by some polythetical characters (Table 1; cp. also Figs 53-59) which, combined, outline a typical congregation in the sense of Smirnov [1923, 1924], i.e. a cluster of close species in a multidimensional character space.

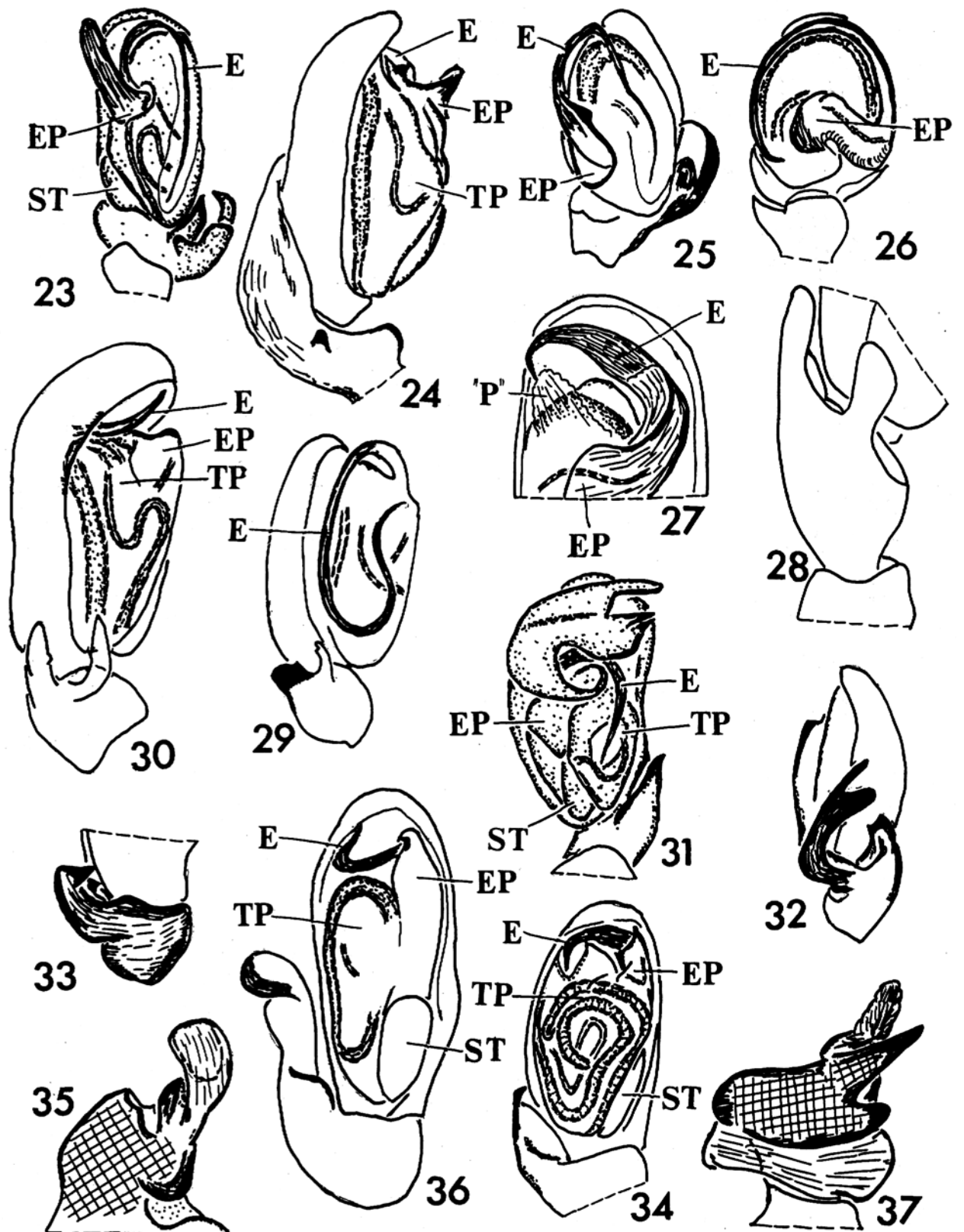
Including a single species, the *zilla*-group (Figs 31, 39) differs exclusively by the male palp structure. It possesses a large bifurcate EP-apophysis ("tegular apophysis", after Ono, 1986). By the structure of the epigyne, according to a recent redescription (Ono, 1986, Figs 6-8), the female of *C. zilla* is close to *C. bakurovi* (the *obesa*-group), displaying no fundamental differences from the set of diagnostic features of the latter group.

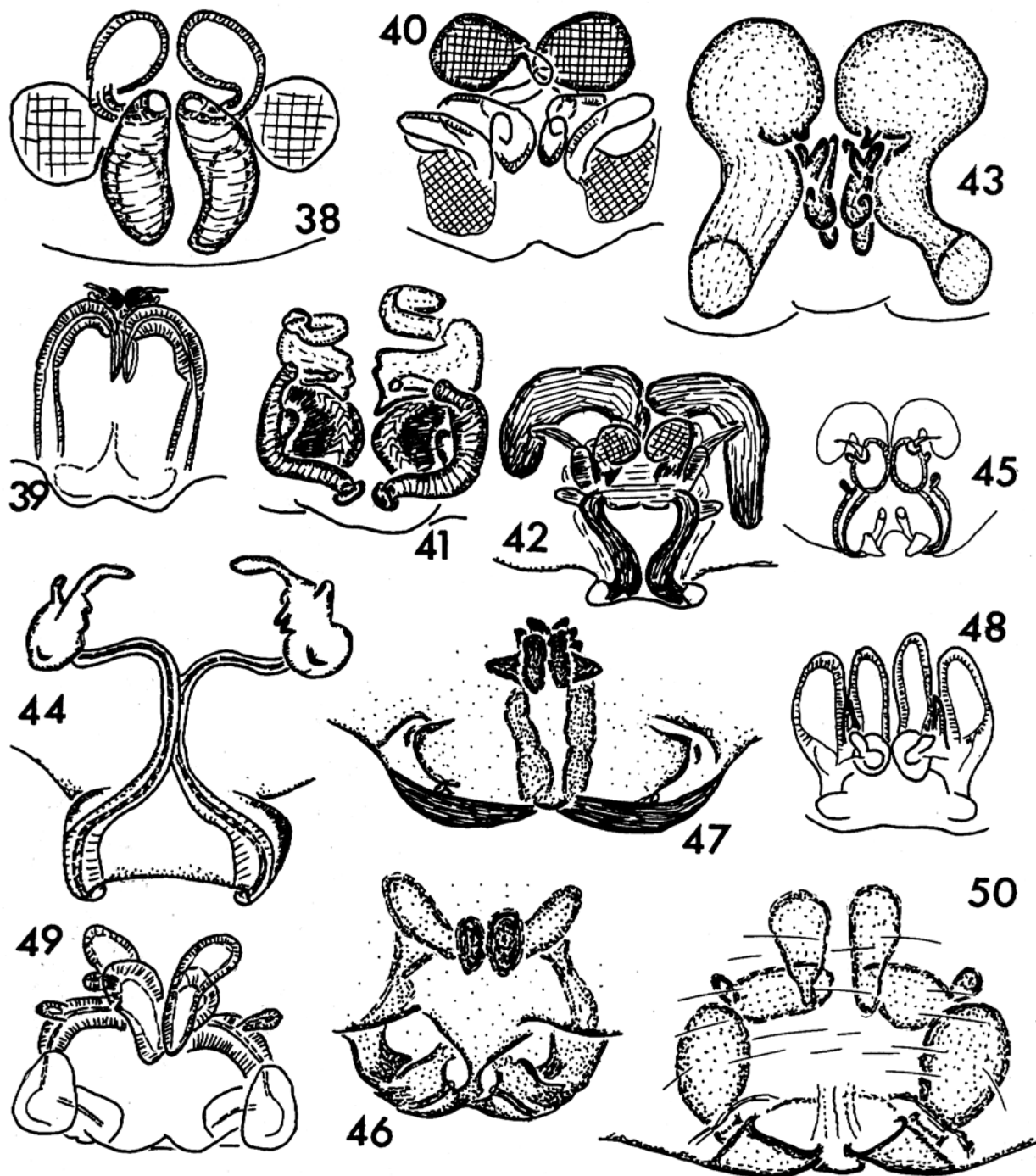
Thus, the separation of 10-11 species-groups

⁵C. Deeleman-Reinhold (personal communication) proposes two species-groups in the Indoneasin fauna of *Paraclubiona*.

Figs 23-37. Structure of male palp in the subgenus *Clubiona* s.str.: 23 — *C. maritima*, 24 — *C. brevipes*, 25 — *C. comta*, 26 — *C. genevensis*, 27 — *C. alpicola*, 28 — *C. saxatilis*, 29 — *C. neglecta*, 30 — *C. japonicola*, 31 — *C. zilla*, 32 — *C. kurilensis*, 33 — *C. furcata*, 34 — *C. sapporensis*, 35 — *C. kunashirensis*, 36 — *C. kimyongkii*, 37 — *C. irinae*. 23,25-26,31,34 — ventral view, 24,29-30,32 — lateral view, 27 — upper half of palp, ventrally, 28 — TiA, laterally, 33 — TiA, dorsally, 35 — TiA, dorsolaterally, 37 — TiA, inner view. 23,33 — after Dondale & Redner, 1982, 24-27,29 — after Wiehle, 1965, 28 — after Thaler, 1981, 31 — after Ono, 1986b, 32 — after Hayashi, Chikuni, 1984. Abbreviations as in Figs 1-11, and "P" — protector-like structure in the group *lutescens*.

Рис. 23-37. Строение пальпы самца в подроде *Clubiona* s.str.: 23 — *C. maritima*, 24 — *C. brevipes*, 25 — *C. comta*, 26 — *C. genevensis*, 27 — *C. alpicola*, 28 — *C. saxatilis*, 29 — *C. neglecta*, 30 — *C. japonicola*, 31 — *C. zilla*, 32 — *C. kurilensis*, 33 — *C. furcata*, 34 — *C. sapporensis*, 35 — *C. kunashirensis*, 36 — *C. kimyongkii*, 37 — *C. irinae*. 23,25-26,31,34 — вентрально, 24,29-30,32 — вид сбоку, 27 — верхняя половина пальпы, вентрально, 28 — TiA, вид сбоку, 33 — TiA, дорсально, 35 — TiA, дорсолатерально, 37 — TiA, вид изнутри. 23,33 — по: Dondale & Redner, 1982, 24-27,29 — по: Wiehle, 1965, 28 — по: Thaler, 1981, 31 — по: Ono, 1986b, 32 — по: Hayashi, Chikuni, 1984. Сокращения как на рис. 1-11, а также "P" — протекторовидная структура в группе *lutescens*.





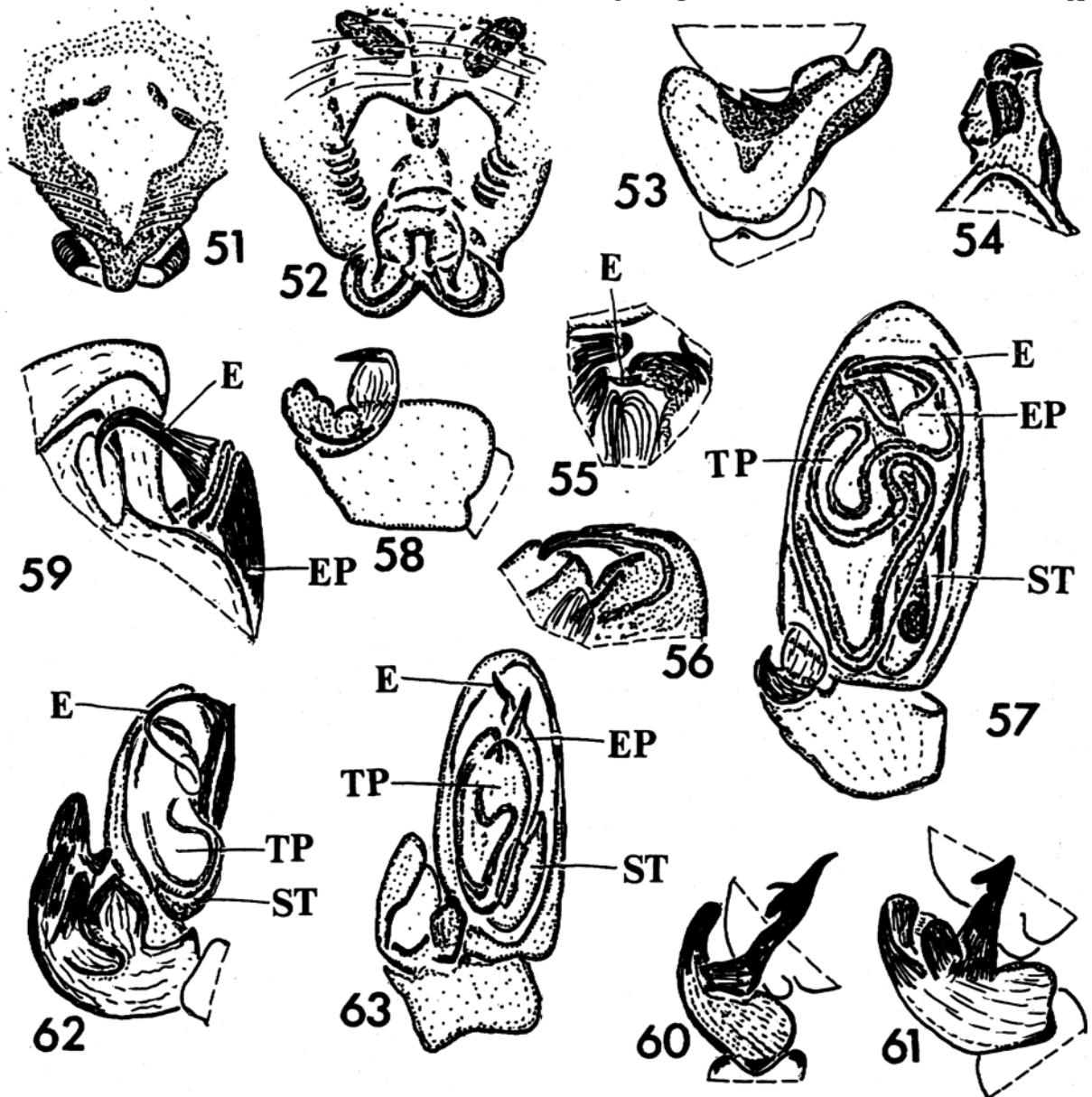
Figs 38-50. Structure of female epigyne and vulva in the subgenus *Clubiona* s.str.: 38 — *C. japonicola*, 39 — *C. zilla*, 40 — *C. latericia*, 41 — *C. wolchongsensis*, 42 — *C. kunashirensis*, 43 — *C. sapporensis*, 44 — *C. kinyongkii*, 45 — *C. chikunii*, 46 — *C. bakurovi*, 47 — *C. irinae*, 48 — *C. phragmitis*, 49 — *C. stagnatilis*, 50 — *C. bashkirica*. 38-45, 48, 49 — vulva, dorsally, 46, 47, 50 — epigyne, 38 — after Gong, 1984, 39 — after Ono, 1986b, 45 — after Hayashi, 1986, 48, 49 — after Wiehle, 1965.

Рис. 38-50. Строение эпигины и вульвы самки в подроде *Clubiona* s.str.: 38 — *C. japonicola*, 39 — *C. zilla*, 40 — *C. latericia*, 41 — *C. wolchongsensis*, 42 — *C. kunashirensis*, 43 — *C. sapporensis*, 44 — *C. kinyongkii*, 45 — *C. chikunii*, 46 — *C. bakurovi*, 47 — *C. irinae*, 48 — *C. phragmitis*, 49 — *C. stagnatilis*, 50 — *C. bashkirica*. 38-45, 48, 49 — вульва, дорсально, 46, 47, 50 — эпигина. 38 — по: Gong, 1984, 39 — по: Ono, 1986b, 45 — по: Hayashi, 1986, 48, 49 — по: Wiehle, 1965.

seems more or less strongly substantiated formally. Others appear to be maintained but tentatively. The *japonicola*-group (Figs 30, 38), with two species, occupies an intermediate position between the *lutescens*- and *similis*-groups. The male is similar to the former group by the shape of a bifurcate TiA, but possesses a comparatively thin embolus, like in the

latter group. The female is distinguished by circular SPTae resembling the simple pattern of the *trivialis*-group, but CT are more sinuous; yet altogether the epigyne is more close to the *similis*-group.

Three other groups, namely the *marmorata*-, *brevipes*-, and *comta*-groups, seem to bias toward the *trivialis*-group, being distinguishable either by a consid-



Figs 51-63. Structure of female epigyne (51-52) and male palp (53-63) in the subgenus *Clubiona* s.str.: 51, 62 — *C. caerulea*, 52, 63 — *C. chabarovi*, 53 — *C. pallidula*, 54 — *C. sopaiensis*, 55 — *C. ezoensis*, 56 — *C. propinqua*, 57, 58 — *C. mayumiae*, 59 — *C. odesanensis*, 60 — *C. subsultans*, 61 — *C. kulczynskii*. 51-52 — epigyne, 53 — TiA, dorsally, 54 — TiA, inner view, 55 — upper part of bulb, ventrolaterally, 56 — upper part of bulb, ventrally, 57, 63 — ventral view, 58 — TiA, ventrolaterally, 59 — upper part of palp, ventrolaterally, 62 — TiA, laterally, 58, 61 — ventrolateral view. 51, 53, 60-62 — after Wiehle, 1965. Abbreviations as in Figs 1-11.

Рис. 51-63. Строение эпигины самки (51-52) и пальпы самца (53-63) в подроде *Clubiona* s.str.: 51, 62 — *C. caerulea*, 52, 63 — *C. chabarovi*, 53 — *C. pallidula*, 54 — *C. sopaiensis*, 55 — *C. ezoensis*, 56 — *C. propinqua*, 57, 58 — *C. mayumiae*, 59 — *C. odesanensis*, 60 — *C. subsultans*, 61 — *C. kulczynskii*. 51-52 — эпигина, 53 — TiA, дорсально, 54 — TiA, вид изнутри, 55 — верхняя часть бульбуса, вентролатерально, 56 — верхняя часть бульбуса, вентрально, 57, 63 — вентрально, 58 — TiA, вентролатерально, 59 — верхняя часть пальпы, вентролатерально, 62 — TiA, вид сбоку, 58, 61 — вентролатерально. 51, 53, 60-62 — по: Wiehle, 1965. Сокращения как на рис. 1-11.

erable enlargement or an underdevelopment of TiA and/or E (Figs 6, 24-26). In contrast to the *trivialis*-group, conjugation of the male and female characters is only slight in the above three species-groups; in the *marmorata*- and *brevipes*-groups, each consisting of paired, very closely related forms, both sexes are known only for a single species apiece. Along with further progress in araneology, all these three groups can prove to be better included into the *trivialis*-group as subgroups, as shown below for the *obesa*-group.

At the moment, subdivision of all *Clubiona* s.str. into species-groups seems impossible, since the exact morphology of the genitalia of some species described from Japan, South Korea and China remains unknown. Moreover, it may be caused by purely morphological reasons, as in the linyphiid genus *Lepthyphantes* [Tanasevitch, 1992].

Some species-groups can be further split into complexes of the third level, namely very compact and morphologically similar species-subgroups. The

degree of morphological generalism of diagnostic (essential) characters is lower than in species-groups, i.e. there are only little differences between species inside such subgroups. Thus, in the *propinqua*-subgroup (*pallidula*-group) all species included, *C. propinqua*, *C. pseudogermanica* and *C. mayumiae*, are almost identical in TiA structure (Fig. 58); such a peculiarity has hitherto remained unknown in other *Clubiona*. Differences between these species lie in body size (with a considerable intergradation), details of E structure (*C. propinqua* — all others, in both cases — Figs 56, 57), and direction of the seminal duct inside EP (*C. pseudogermanica* — *C. mayumiae*). Female distinguishing features are also very slight. Similarly, the *genevensis*-subgroup (*compta*-group) (Figs 20, 26) can be characterized solely by some minor differences in a generally uniform structure of the male palp and endegyne.

Besides that, a lot of groups have reasonably long been established within the *obesa*-group. The latter is quite species-rich and differs only by a tendency of variation in some characters (see above), i.e. a highly dynamic archetype. Separation of some smaller complexes seems to be useful there from a purely practical viewpoint. Besides subgroups encompassing two and more species, certain species exist in the *obesa*-group that display highly disjunct and stereospecifically arranged genitalia. Thus, *C. bakurovi* and *C. irinae* also belong in species-subgroups of their own. Altogether, no fewer than six subgroups can be established within the Palearctic *obesa*-group: the *akagiensis*- (Japan), the *latericia*-, the *sapporensis*-, the *corrugata*-, the *bakurovi*-, and the *irinae*-subgroups (for the geographical distribution of the last five of these, see Mikhailov, 1992).

A total subdivision of all *Clubiona* species-groups seems impossible due to morphological reasons.

Establishment of three levels of infrageneric groupings (subgenus — species-group — species-subgroup) is undertaken here for ordination both of generalism and the extent of morphological differences. Nonetheless, at each level the groupings themselves differ considerably by the extent of morphological similarity between species included. Thus, at the subgeneric level, the greatest degree of congeneric similarity seems to occur amongst *Japoniona* species, while at the species-group one among the *reclusa*-group members. This further supports the specificity of the meronomic-taxonomical relation, for a considerably more widely distributed feature is known to be a general meronomic-taxonomical inconformity [Lyubarsky, 1991].

The female spider genitalia have traditionally been viewed as less variable than the male ones [Eberhard, 1985: 30]. This trend is especially well-pronounced in araneoid spiders, such as the Linyphiidae, to a lesser extent also in the Theridiidae. The same phenomenon is characteristic of *Clubiona* as well.

Expressing it more exactly, at the species level the degree of generalism of differences (differential characters, see Nelson & Platnick, 1981: 160-164) in *Clubiona* female genitalia can be stated to be lower than that in the male genitalia.

Yet, traited generally, as accepted for all spiders, this statement ignores certain differences in the

capacity for a change. Certainly there is less room for genitalic variability in spider females than in males. Being surrounded from three sides by abdominal organs, the epigyne is actually a structure rather limited in volume; the shape of its cavities and canals can be only circular, ovoid, or tubular. Whereas the growing capacities of the male bulb are far less stringent, as well illustrated e.g. by the subgenus *Paraclubiona*. Not being hollow, the apophyses of the palp tibia, tegulum, and embolar part can be considerably more slender, acute, branched, etc., that is, much more variable as compared to vulval canals.

The above statement that the range of variability differs in male and female genitalia has been introduced in a discussion of the role of the key-lock (hand-glove) principle in sexual character selection [Eberhard, 1985]. Yet this circumstance seems unimportant, because there are many other reasons to reject the key-lock principle.

Characteristics of infrageneric groupings

Subgenus *Paraclubiona* (Lohmander, 1945).

Type species: *Clubiona corticalis* (Walckenaer, 1802).

Diagnosis. The male differing by the tegular enlargement of the bulb (Figs 2-3), the female by the frontal position of CO (Fig. 12).

Description. Male. TiA weakly developed, of relatively simple shape. Bulb large, protruding. Conductor, if existing, of tegular nature, weakly sclerotized, completely separated from tegulum, lacking in *C. corticalis*, *C. cirrosa*. Tegular apophysis weakly sclerotized, large (*C. kurosawai* — Fig. 3), small (*C. cirrosa*) or lacking (*C. corticalis*, *C. pyrifer*). E fili-, spiniform or very short and almost missing (*C. pyrifer*), directed straightly distad or spiralling at tip (*C. cirrosa*).

Female. CO in fore part of epigyne, removed far away from epigastric furrow. CT directed caudally. Atrium vesiculiform, poorly visible, positioned in hind part of genitalia. SPT tubular, sometimes circular, considerably less in size than atrium.

Clubiona (Paraclubiona) corticalis (Walckenaer, 1802)

Clubiona (Paraclubiona) chakrabarti Majumder et Tikader, 1991

Clubiona (Paraclubiona) cirrosa Ono, 1989

Clubiona (Paraclubiona) concinna (Thorell, 1887)

? *Clubiona (Paraclubiona) drassodes* O. Pickard-Cambridge, 1874

Clubiona (Paraclubiona) kurosawai Ono, 1986

Clubiona (Paraclubiona) lyriformis Song et M. Zhu, 1991

Clubiona (Paraclubiona) melanosticta Thorell, 1890

Clubiona (Paraclubiona) moralis Song et M. Zhu, 1991

Clubiona (Paraclubiona) pyrifer Schenkel, 1936

Clubiona (Paraclubiona) shillongensis Majumder et Tikader, 1991

Clubiona (Paraclubiona) yaginumai Hayashi, 1989

Subgenus *Japoniona* Mikhailov, 1990.

Type species: *Clubiona japonica* L. Koch, 1878.

Diagnosis. The male differing by the characteristic shape of the tegular conductor (Fig. 4). The genital groove or CO placed in the middle of the epigyne. CT directed downwards, either retracted in the depth of the epigyne or shifted a little forwards (Fig. 13).

Description. Male. TiA strongly sclerotized, not branched, little, thin or strongly attenuating closer to top. Bulb non-protruding. Conductor tegular, considerably larger than E, weakly sclerotized, of a characteristic

shape. Tegular apophysis of a characteristic shape (hook- or hammer-like), placed in distal part of tegulum. E lori- or filiform, directed distad, then retrolaterad.

Female. Genital groove either large, sometimes partly divided, or missing (*C. vigil*). CO and CT as in Diagnosis. Atrium either large, vesiculiform, circular, positioned in hind part of genitalia (*C. vigil*) or oblong-ovoid and placed in fore part. SPT either considerably less in size than atrium and situated near its back part or almost equal in size to atrium and situated in front of it (*C. vigil*).

Clubiona (Japoniona) japonica L. Koch, 1878

Clubiona (Japoniona) flavipes (Saito, 1939)

Clubiona (Japoniona) vigil Karsch, 1879

Subgenus *Bicluona* Michailov, 1994.

Type species: *Clubiona jucunda* (Karsch, 1879).

Diagnosis. The male differing by the singular position of E mostly lying between the bulb and the cymbium (Fig. 5). The female differing from that of *Paraclubiona* and *Japoniona* by CO placed caudally and CT directed forwards (Fig. 14).

Description. Male. TiA short, not branched. Tegular apophysis rectangular, not unciform. Tegular conductor missing. E filiform.

Female. A large genital groove in hind part of epigyne. CT directed forwards, sinuous. SPT large, vesiculiform.

Clubiona (Bicluona) jucunda (Karsch, 1879)

Subgenus *Clubiona* sensu stricto.

Type species: *Clubiona pallidula* (Clerck, 1757).

Diagnosis. The male differing by the conductor of embolar nature combined with the sclerotized tegular apophysis wanting; the bulb is either usually not surpassing the cymbium or enlarged due to EP. The female differing by the position of CO either in the hind part or at the rear edge of the epigyne as well as by CT directed forwards.

Description. Male. TiA usually well-developed and sclerotized, often of a complex shape. Bulb usually elongated. Embolar conductor not always expressed. E of variable shape, from aciculi- and aculeiform to oblong-loriform, directed retrolaterad or proximad, sufficiently long coiling around tegular tip.

Female. CT more often long. Atrium sclerotized, usually placed in fore part of genitalia. SPT ovoid, circular or tubular, sometimes bipartite and strongly curved sagittally.

The *trivialis*-group

Diagnosis. The male differing by the not branched, wide, flat or almost flat TiA, weakly angled or dentate, rarely attenuating (Figs 8-10). The female differing by the simple structure of circular or ovoid SPTae combined with CO brought close together or fused into a single groove, and CT straight or almost straight (Fig. 15).

Description. Male. TiA as in Diagnosis, tending to enlarge in *C. rostrata* and *C. transbaicalica*. EP with a small apophysis near EB, sometimes bearing 1-3 teeth. EB covered by EP-apophysis (except *C. insulana*). E placed totally in apical part of bulb, arched around or angled across tegular tip, sometimes stretching proximad along a membranous, slightly depressed "conductor" up to midway of bulb (*C. trivialis*, *C. rostrata*). Seminal duct relatively short.

Female. Hind edge of epigyne usually projecting a little beyond epigastric furrow (except *C. moesta*). CO small, placed near hind edge of epigyne, fused at latter's midline, rarely separated from, but situated very close to, each other, as in *C. quebecana* and *C. pygmaea*. CT thin

or medium-sized, straight or slightly arched. Atrium positioned just in front of SPT. SPT unipartite, ovoid or circular. Cover of genital plate thin, usually non-rugose (except *C. pygmaea*).

Clubiona (Clubiona) trivialis C.L. Koch, 1843

Clubiona (Clubiona) amurensis Michailov, 1990

Clubiona (Clubiona) aspervida Ono, 1992

Clubiona (Clubiona) baimaensis Song et M. Zhu, 1991

Clubiona (Clubiona) basarukini Michailov, 1990

Clubiona (Clubiona) diversa O. Pickard-Cambridge, 1862

Clubiona (Clubiona) duoconca Zhang et Hu, 1991

Clubiona (Clubiona) insulana Ono, 1989

Clubiona (Clubiona) janae Edwards, 1958

Clubiona (Clubiona) juvenis Simon, 1878

Clubiona (Clubiona) moesta Banks, 1896

Clubiona (Clubiona) pygmaea Banks, 1892

Clubiona (Clubiona) quebecana Dondale et Redner, 1976

Clubiona (Clubiona) rostrata Paik, 1985

Clubiona (Clubiona) subrostrata Zhang et Hu, 1991

Clubiona (Clubiona) subtilis L. Koch, 1866

Clubiona (Clubiona) subtrivialis Strand, 1906

Clubiona (Clubiona) transbaicalica Michailov, 1992

? *Clubiona (Clubiona) yangmingensis* Hayashi et Yoshida, 1993

The *abboti*-group

Diagnosis. Male (Fig. 11): apophysis of EP strongly developed, convex ventro-prolaterally and concave dorso-retrolaterally, TiA bifurcate, not flat. Female (Fig. 16): CO either paired or fused into genital groove, CT semi-circular; genital plate rugose, protruding beyond epigastric furrow.

Description. Male. TiA as in Diagnosis, with ventral branch always directed parallel to main axis. Base of EP-apophysis placed in middle part of bulb, this apophysis covering EB. E long, arched around or angled across bulb tip; E top lying in proximal half of bulb (except *C. angulata*). Bulb surface with a membranous conductor.

Female. CO large (only in *C. angulata* small), either separated (in most species) or fused into genital groove, either partly (*C. opeongo*, *C. littoralis*) or totally (*C. catawba*). CT arched or sinuous (*C. angulata*). Other features as in Diagnosis.

Clubiona (Clubiona) abboti L. Koch, 1866

Clubiona (Clubiona) adjacens Gertsch et Davies, 1936

Clubiona (Clubiona) angulata Dondale et Redner, 1976

Clubiona (Clubiona) bishopi Edwards, 1958

Clubiona (Clubiona) catawba Gertsch, 1941

Clubiona (Clubiona) dyasia Gertsch, 1941

Clubiona (Clubiona) estes Edwards, 1958

Clubiona (Clubiona) gertschi Edwards, 1958

Clubiona (Clubiona) johnsoni Gertsch, 1941

Clubiona (Clubiona) kagani Gertsch, 1941

Clubiona (Clubiona) kastoni Gertsch, 1941

Clubiona (Clubiona) kiowa Gertsch, 1941

Clubiona (Clubiona) littoralis Banks, 1895

Clubiona (Clubiona) marna Roddy, 1966

Clubiona (Clubiona) mutata Gertsch, 1941

Clubiona (Clubiona) newmani Ivie et Barrows, 1935

Clubiona (Clubiona) nicholsi Gertsch, 1941

Clubiona (Clubiona) odelli Edwards, 1958

Clubiona (Clubiona) opeongo Edwards, 1958

Clubiona (Clubiona) oteroana Gertsch, 1941

Clubiona (Clubiona) pikei Gertsch, 1941

Clubiona (Clubiona) plumbi Gertsch, 1941

Clubiona (Clubiona) pomoa Gertsch, 1941

Clubiona (Clubiona) procteri Gertsch, 1941

Clubiona (Clubiona) rhododendri Barrows, 1945

Clubiona (Clubiona) saltitans Emerton, 1919

The *marmorata*-group

Diagnosis. The male differing both by the strongly

developed, flat, wide TiA and embolar conductor (Fig. 6). The female differing by CO widely separated from each other combined with CT almost straight and the epigyne strongly sclerotized.

Description. Male. TiA attaining ca. 0.4-0.5 of cymbial length. Conductor slightly protruding beyond cymbium and covering latter's base in ventral view. E coiled around tegular tip, not stretching proximally. Seminal duct relatively short.

Female (known only in *C. marmorata*). CO small. CT slightly arched. Atrium bordering SPT, circular. SPT unipartite, cylindrical, slightly narrowed in middle part, stretching along epigynal midline. Epigyne strongly sclerotized in hind part, with two depressions in the middle presumably destined for TiA fixation during copulation.

Clubiona (Clubiona) marmorata L. Koch, 1866

Clubiona (Clubiona) hyrcanica Mikhailov, 1990

The *maritima*-group

Diagnosis. Male: EP with a large spur-like apophysis protruding beyond cymbium (Fig. 23). Female: CO slit-like, CT sinuous, SPTae adjoined, hind edge of epigyne strongly sclerotized (Fig. 17).

Description. Male. TiA with three branches, each not longer than 1/3 of cymbial length. EP-apophysis covering EB. E long, arched around bulb tip, then stretching proximad along a membranous "conductor".

Female. Main features see in Diagnosis. CT thin, long, first diverged, then converged.

Clubiona (Clubiona) maritima L. Koch, 1866

The *brevipes*-group

Diagnosis. Male differing by the characteristically bifurcate EP-apophysis (Fig. 24), female by CT diverging from the median groove combined with the simple circular SPTae (Fig. 18).

Description. Male. TiA flat, either subdivided at tip (*C. brevipes*) or attenuating and curved (*C. alexeevi*). EP-apophysis bifurcate, in lateral view directed (sub)rectangularly to bulb surface, not covering EB. E arched around tegular tip. Seminal duct relatively short.

Female (known only in *C. brevipes*). CO fused into genital groove of a characteristic multiangular shape. CT diverged laterad, then curved forward. Atrium a little bigger than SPT, bordering it. SPT unipartite, circular.

Clubiona (Clubiona) brevipes Blackwall, 1841

Clubiona (Clubiona) alexeevi Mikhailov, 1990

The *comta*-group

Diagnosis. The male (Figs 25-28) differing by the total or almost total fusion of EP-apophysis with E itself combined with the embolar tip directed proximad and reaching the base of the bulb. The female (Figs 19-20) differing by the total or almost total fusion of CO combined with CT bordering each other and parallel in the beginning, then strongly curved. A considerable extent of CT corresponding to the length of the male E.

Description. Male. TiA flat, curved, attenuating in *C. comta* (Fig. 25), simple and short in the *genevensis*-subgroup (Fig. 26). EP-apophysis well-visible only in *C. comta* at EB. EB solid, sometimes overgrowing prolaterad, a little beyond cymbium (*C. comta*, *C. genevensis*). E long, curved around tegular tip and directed proximad. Seminal duct relatively short.

Female. Genital groove either small (*C. comta*, Fig. 19) or large (*C. genevensis* etc. — Fig. 20). CT parallel

or almost parallel to each other in the beginning (*C. minor*, *C. pseudominor*), then curved ventrad in fore part of endegyne to return backwards parallel to each other (except *C. pseudominor*), but quickly arching and diverging laterad. Atrium bordering SPT, both simple, ovoid.

Clubiona (Clubiona) comta C.L. Koch, 1839

Clubiona (Clubiona) decora Blackwall, 1859

Clubiona (Clubiona) diniensis Simon, 1878

Clubiona (Clubiona) genevensis L. Koch, 1866

Clubiona (Clubiona) leucaspis Simon, 1932

Clubiona (Clubiona) minor Wunderlich, 1987

Clubiona (Clubiona) parallela Hu et Li, 1988

Clubiona (Clubiona) pseudominor Wunderlich, 1987

Clubiona (Clubiona) tenerifensis Wunderlich, 1991

Clubiona (Clubiona) vegeta Simon, 1878

Clubiona (Clubiona) wunderlichi Mikhailov, 1992

Clubiona (Clubiona) zhangmuensis Hu et Li, 1988

The *genevensis*-subgroup

Diagnosis. The male differing by the weakly developed and non-furcate TiA as well as by a dark spot of thick hairs on the prolateral side of the cymbium (Fig. 26). The female differing by the large genital groove characteristically semi-circular or inverted cordiform (Fig. 20).

Description of both male and female coincides with the group description including the subgroup diagnosis.

C. genevensis, *C. decora*, *C. diniensis*, *C. leucaspis*, *C. minor*, *C. parallela*, *C. pseudominor*, *C. tenerifensis*, *C. vegeta*, *C. wunderlichi*, *C. zhangmuensis*.

The *lutescens*-group

Diagnosis. The male differing by the bifurcate convex TiA (Fig. 28) combined with the wide E and missing embolar conductor (Fig. 27). The female differing by the straight or almost straight CT curved at the end combined with the ovoid atrium and tubular, unipartite SPT curved from the depth of the vulva to its surface (Fig. 21).

Description. Male. TiA with two convex branches of an almost equal length (in *C. pseudosaxatilis*, dorsal one a little larger). EP-apophysis fused with EB, so latter considerably wide; only in *C. frutetorum* the border between them is visible. E beginning in proximal or middle part of tegulum, directed prolaterodistad, then arched around tegular tip and moving on retrolaterad along alveolar wall, sometimes coiling at bulb tip; often with a thin crest. Membranous tegular "conductor" expressed as a protector-like tegular apophysis ("P" in Fig. 28). Seminal duct long.

Female. Well-visible CO placed in hind part of genital plate. CT wide, directed forward and a little laterad. SPT tubular, thin or thick, curved outwards from depth of vulva, thus looking as if bipartite. Atrium circular, positioned in front of SPT, more median in *C. lutescens* and *C. golovatchi*, more lateral in others. Atriospermathecal tube short and wide. Genital plate smooth, usually without groove (except *C. riparia*; poorly expressed in *C. lutescens* and *C. saxatilis*).

Clubiona (Clubiona) lutescens Westring, 1851

Clubiona (Clubiona) alpicola Kulczyński, 1882

Clubiona (Clubiona) andreinii Caporaccio, 1936

Clubiona (Clubiona) frutetorum L. Koch, 1866

Clubiona (Clubiona) golovatchi Mikhailov, 1990

Clubiona (Clubiona) hilaris Simon, 1878

Clubiona (Clubiona) prozyskii Mikhailov, 1995

Clubiona (Clubiona) pseudosaxatilis Mikhailov, 1992

Clubiona (Clubiona) riparia L. Koch, 1866

Clubiona (Clubiona) saxatilis L. Koch, 1867

Clubiona (Clubiona) terrestris Westring, 1851

The *similis*-group

Diagnosis. The male differing by the weakly convex, bifurcate TiA with the ventral branch more thin, narrow and attenuating, combined with a thin E (Fig. 29) and the absence of a conductor. The female differing by CT long, strongly curved in distal half, combined with the simple ovoid or tubular SPT not curved in the depth of the vulva (Fig. 22).

Description. Male. TiA bifurcate, with the ventral branch either thin (*C. similis*, *C. neglecta*, *C. aducta*, *C. pseudosimilis* — Fig. 29) or attenuating (*C. germanica*, *C. congenilis*). EB apparently fused with EP-apophysis. E thin, arising from the middle or distal part of bulb, directed prolaterodistad, then arched around or angularly across tegular tip, moving on proximad, arching on ventral bulb surface (in the upper half in most species, over all surface returning to EB in *C. neglecta*).

Female. CO opening mostly at hind edge of epigyne, sometimes in groove in epigynal hind part (*C. germanica*, *C. congenilis*). CT wide, directed parallel forward or slightly diverging (*C. similis*, *C. aducta* — Fig. 22), then coiling several times in middle part of vulva, converging toward midline and finally a little diverging. Atrium circular and ovoid, placed in front of SPT and then more laterally. SPT simple, ovoid, sometimes considerably less in size than atrium (*C. germanica*) or completely circular (*C. pseudosimilis*), rarely tubular (*C. similis*). Epigynal surface smooth.

- Clubiona* (*Clubiona*) *similis* L. Koch, 1866
Clubiona (*Clubiona*) *aducta* Simon, 1932
Clubiona (*Clubiona*) *congenilis* Kulczyński, 1913
Clubiona (*Clubiona*) *germanica* Thorell, 1871
Clubiona (*Clubiona*) *neglecta* O. Pickard-Cambridge, 1862
Clubiona (*Clubiona*) *pseudoneglecta* Wunderlich, 1994
Clubiona (*Clubiona*) *pseudosimilis* Michailov, 1990

The *japonicola*-group

Diagnosis. By the structure of the male genitalia, the group is close to the *lutescens*-group differing by the thin E or more thin TiA (Fig. 30); by the structure of the female genitalia it is close to the *similis*-group, distinguished by the circular SPTae (Fig. 38).

Description. Male. TiA with two processes separated from their bases. EP-apophysis passes on directly into E, in *C. japonicola* a little covering the latter's base. E in the upper half of the bulb, directed retrolaterad, then prolaterodistad, exceeding forward the alveola's limits. In *C. yasudai* a membranous "conductor" expressed as a tegular apophysis. Seminal duct relatively short.

Female. CO separated from each other, very large, positioned in hind part of the genital plate. CT wide, first directed forward, then in the middle part of the vulva rectangularly laterad outward. Atrium circular, placed in front of SPT, closer to epigynal midline. SPT simple, circular, a little larger than atrium.

- Clubiona* (*Clubiona*) *japonicola* Bösenberg et Strand, 1906.
Clubiona (*Clubiona*) *yasudai* Ono, 1991.

The *zilla*-group

Diagnosis. The male differing by the large branched EP-apophysis being wider than bulb (Fig. 31). Female differing by the presence of a transverse furrow with slit-like CO at its corners (Fig. 39).

Description. Male. TiA wide, short, thick. EP-apophysis large, with 2 branches in the upper third, the lower branch trifurcate. E moderately thick, arising prolaterally, then arched around the bulb top and ending at its lower third. Membranous "conductor" present.

Female. CO slit-like. CT straight, converging to the middle of epigyne, more thin near atria. Atrium and SPT

small. Atrium tubular, SPT circular, its diameter not exceeding 1/5 of epigynal width.

- Clubiona* (*Clubiona*) *zilla* Dönitz et Strand, 1906.

The *obesa*-group

Diagnosis. The male differing by the wide TiA usually convex ventrally and concave dorsally (Figs 32-33, 35-36). Sometimes TiA turned around its axis or strongly developed. E thin, usually supplied with a membranous "conductor" on tegular surface. Female differing by cavity-like CO usually situated at the posterior angles of the genital plate, combined with unparallel CT (Figs 40-47).

Description. Male. TiA see Diagnosis, it slightly torsate, especially so in the *akagiensis*-subgroup. TiA can be divided into two weak branches or strongly developed, either simple (*C. bakurovi*) or strongly branched (*C. kurilensis*, *C. irinae* — Figs 32, 37). EP-apophysis of different shape, being close to EB (except *C. obesa* and *C. mixta*). E beginning from bulb prolaterally, arched around its distal top (except the *latericia*-subgroup), thin, obtuse apically in *C. obesa* and *C. mixta*. Conductor lacking only in the *latericia*-subgroup. Seminal duct of medium length.

Female. CO cavity-like, positioned near posterior lateral angles of genital plate, only in *C. spiralis* slit-like and situated in the middle of epigyne. CT from narrow to moderately wide, not parallel; if almost parallel, as in the *sapporensis*-subgroup (Fig. 43), converging to the epigyne median line. Atrium circular or ovoid, bordering SPT. SPT either unipartite circular, ovoid, tubular, or tends to be bipartite (*C. kurilensis*, *C. praematura*, especially the *sapporensis*-subgroup). Genital plate wide and smooth, slightly wrinkled in *C. kurilensis*, usually incised posteriorly.

- Clubiona* (*Clubiona*) *obesa* Hentz, 1847
Clubiona (*Clubiona*) *aciformis* Zhang et Hu, 1991
Clubiona (*Clubiona*) *akagiensis* Hayashi, 1985
Clubiona (*Clubiona*) *bakurovi* Michailov, 1990
Clubiona (*Clubiona*) *bryantae* Gertsch, 1941
Clubiona (*Clubiona*) *charitonovi* Michailov, 1990
Clubiona (*Clubiona*) *chechtsirica* Michailov, 1995
Clubiona (*Clubiona*) *chikunii* Hayashi, 1986
Clubiona (*Clubiona*) *chippewa* Gertsch, 1941
Clubiona (*Clubiona*) *corrugata* Bösenberg et Strand, 1906
Clubiona (*Clubiona*) *eskovi* Michailov, 1995
Clubiona (*Clubiona*) *furcata* Emerton, 1919
Clubiona (*Clubiona*) *fusoidea* Zhang, 1993
Clubiona (*Clubiona*) *fuzhouensis* Gong, 1985
Clubiona (*Clubiona*) *ikedai* Ono, 1993
Clubiona (*Clubiona*) *inaensis* Hayashi, 1989
Clubiona (*Clubiona*) *irinae* Michailov, 1991
Clubiona (*Clubiona*) *kimyongkii* Paik, 1990
Clubiona (*Clubiona*) *kunashirensis* Michailov, 1990
Clubiona (*Clubiona*) *kurenshikovi* Michailov, 1995
Clubiona (*Clubiona*) *kurilensis* Bösenberg et Strand, 1906
Clubiona (*Clubiona*) *latericia* Kulczyński, 1926
? *Clubiona* (*Clubiona*) *lena* Bösenberg et Strand
Clubiona (*Clubiona*) *logunovi* Michailov, 1990
Clubiona (*Clubiona*) *manshanensis* M. Zhu et An, 1988
Clubiona (*Clubiona*) *marusiki* Michailov, 1990
Clubiona (*Clubiona*) *maya* Hayashi et Yoshida, 1991
Clubiona (*Clubiona*) *microsapporensis* Michailov, 1990
Clubiona (*Clubiona*) *mimula* Chamberlin, 1928
Clubiona (*Clubiona*) *mixta* Emerton, 1980
Clubiona (*Clubiona*) *nenilini* Michailov, 1995
Clubiona (*Clubiona*) *paiki* Michailov, 1991
? *Clubiona* (*Clubiona*) *paralena* Michailov, 1995
Clubiona (*Clubiona*) *phragmitoides* Schenkel, 1963
Clubiona (*Clubiona*) *praematura* Emerton, 1909
Clubiona (*Clubiona*) *rileyi* Gertsch, 1941
Clubiona (*Clubiona*) *sapporensis* Hayashi, 1986
Clubiona (*Clubiona*) *spiralis* Emerton, 1909

Clubiona (Clubiona) subborealis Mikhailov, 1992
Clubiona (Clubiona) tsurusakii Hayashi, 1987
Clubiona (Clubiona) uenoi Ono, 1986
Clubiona (Clubiona) wolchongsensis Paik, 1990
Clubiona (Clubiona) yoshidai Hayashi, 1989

The *latericia*-subgroup

Diagnosis. The male differing by the short E, not wider than 2/3 of bulb, combined with TiA typical in the group. The female differing by the strong sclerotization of the inner structure (Fig. 40) and the SPTae ovoid or tubular (*C. kunashirensis* — Fig. 42), positioned in the fore part of the genitalia.

Description. Male. TiA bifurcate from base (*C. latericia*, *C. bryantae*) or with the ventral branch more strongly developed (*C. kunashirensis* — Fig. 35). EP-apophysis covering EB, sometimes small (*C. kunashirensis*, *C. maya*). E usually short, not longer than 1/2 of bulb width (2/3 in *C. tsurusakii*), straight, acute. Conductor lacking (except *C. tsurusakii*).

Female. CO consist of wide depressions (*C. latericia* — Fig. 40, *C. bryantae*) or small grooves (*C. tsurusakii*, *C. kunashirensis*, *C. wolchongsensis* — Fig. 42), sometimes positioned beyond the epigastric furrow on a small epigynal outgrowth (*C. kunashirensis*, weaker in *C. maya*). CT sinuous, more rarely almost straight (*C. kunashirensis*). Mutual disposition of atrium and SPT obscure due to the absence of sufficient material.

C. latericia, *C. bryantae*, *C. kunashirensis*, *C. maya*, *C. tsurusakii*, *C. wolchongsensis*

The *sapporensis*-subgroup

Diagnosis. The male differing by the presence of one (ventral) branch of TiA turned typically for the total group, combined with the short E, approximately equal to the bulb width (Fig. 34). The female differing by the complex structure of SPT supplied with diverse outgrowths (Fig. 43).

Description. Male. TiA see Diagnosis. EP-apophysis covering EB partly or completely. E short, directed retrolaterad, then proximad. Membraneous "conductor" present.

Female. Ovoid CO positioned near hind edge of genital plate. CT sometimes almost parallel, a little converging. Tubular SPT with an outgrowth, strongly curved from the depth of vulva outward, so in a transverse plane it seems bipartite. Atrium larger than SPT, ovoid, positioned more laterally, as in the *pallidula*-group.

C. sapporensis, *C. charitonovi*, *C. eskovi*, *C. fuzhouensis*, *C. manshanensis*, *C. microsapporensis*, *C. nenilini*

The *corrugata*-subgroup

Diagnosis. The male differing by the long simple TiA sometimes reaching midlength of the cymbium, combined with the relatively short E (Fig. 36). The female differing by the thin and long CT, small atria and SPTae (Fig. 44).

Description. Male. TiA long, convex retrolaterally, concave prolaterally, sometimes spiralling (*C. kimyongkii*). E short, lying free above tegulum in alveolum (*C. kimyongkii*), or curved around tegulum (*C. corrugata*); in the last case membraneous conductor is weakly developed. In *C. kimyongkii*, tip of E curved proximad, as in the *japonicola*-group. EP-apophysis covering EB (*C. kimyongkii*) or not, carrying two teeth (*C. corrugata*). Seminal duct long (*C. corrugata*) or of medium length (*C. kimyongkii*).

Female. CO cavity-like, opening at hind edge of genital plate or circular, positioned in its hind part (*C.*

phragmitoides). CT narrow, directed laterad, then converging and becoming parallel to each other. SPT and atrium placed on sides of vulva or in its middle (*C. corrugata*). SPT irregularly ovoid (*C. corrugata*), tubular, either of medium length (*C. kimyongkii*, *C. kurenshevikovi*) or strongly elongate (*C. phragmitoides*). Atrium circular, bordering SPT, larger than it (*C. kimyongkii*, *C. kurenshevikovi*) or smaller (*C. corrugata*). By CT structure, the species of this group resemble *C. kurilensis*.

C. corrugata, *C. kimyongkii*, *C. kurenshevikovi*, *C. phragmitoides*

The *akagiensis*-subgroup

Diagnosis. The male differing by the tip of TiA curved downwards, combined with E thin and attenuating, directed retrolaterad or retrolatero-apicad, as well as by the considerable EP-apophysis. The female differing by CT semicircular (Fig. 45), directed backwards in *C. chikunii* and *C. ikedai*, then laterad, forward and to the midline of the epigyne.

Description. Male. Curvature of TiA tip mostly expressed in *C. akagiensis* and *C. chikunii*. E directed retrolaterad in *C. akagiensis*, almost retrolaterad in *C. chikunii*, and retrolatero-apicad in *C. ikedai*, its length not exceeding bulb width. EP-apophysis directed retrolaterad in *C. akagiensis*, retrolatero-apicad in *C. chikunii*, and apicad in *C. ikedai*.

Female. CO small, rounded (*C. chikunii*, *C. ikedai*), positioned in the middle (*C. ikedai*), hind (*C. chikunii*) part of epigyne or at its hind edge (*C. akagiensis*), which is inserted in two latter species. Atrium small in *C. chikunii* and *C. ikedai*, in *C. akagiensis* its disposition remains obscure due to the absence of material available for study. SPT ovoid (*C. akagiensis*) or tubular.

C. akagiensis, *C. chikunii*, *C. ikedai*

The *bakurovi*-subgroup

Diagnosis. The male differing by the strong indivisible TiA, the large tooth on the long EP-apophysis, and by the absence of a "conductor". The female (Fig. 46) differing by the strongly sclerotized ridge (septum) positioned along the midline in the hind part of the genital plate, combined with the depression in the plate serving for fixation of the male palp during copulation.

Description. Male. TiA strong, convex retrolaterally and concave prolaterally. E positioned in distal part of bulb, curved behind tegulum. EP-apophysis large and long, covering EB, with a large tooth.

Female. CO positioned near midline of epigyne, divided by a strongly sclerotized longitudinal ridge (Fig. 46). CT directed laterad, then forward, widely separated from each other, almost parallel. SPT simple, arched, atrium bordering it.

A strongly chitinized hind edge of epigyne as much as two strongly sclerotized grooves near hind edge of genital plate obviously serving as a support for huge male TiA during copulation. Inner membrane of female genitalia, almost transparent in most *Clubiona* species, also strongly sclerotized here. Epigyne projecting beyond epigastric furrow, weakening the total construction.

C. bakurovi

The *irinae*-subgroup

Diagnosis. The male differing by the strong and strongly subdivided TiA (Fig. 37) and long E. The female differing by the strong sclerotization of the hind edge of the genital plate (Fig. 47) not hanging over the

epigastric furrow, combined with CT being wide, converging to the middle of the epigyne and then almost parallel.

Description. Male. TiA large, carrying one external and two internal branches. EP-apophysis covering EB. E long, occupying 2/3 of bulb length. Membranous "conductor" present.

Female. CO rounded, with curved furrows in genital plate flowing into them from lateral sides. Direction of CT see in Diagnosis. SPT complex, curved, tubular, bordering circular atrium.

Hind part of genital plate strongly sclerotized correspondingly to the strong male TiA.

C. irinae

The *pallidula*-group

Diagnosis. The male differing by the thick, sometimes weakly-divided TiA (Figs 53-54, 58) and short E; when E long, EP-apophysis carrying a double ridge (Fig. 59). The female differing by the SPTae distinctly bipartite, tubular, rarely ovoid (Fig. 48).

Description. Male. TiA thick, with a cluster of short branches depressed from inwards (*C. hummeli*, in *C. pallidula* there are two branches, but one of them is semi-transparent, thin and poorly visible — Fig. 53), without depressions (*C. odesanensis*), or with two distinct branches (*C. phragmitis*, *C. zacharovi*, the *propinqua*-subgroup — Fig. 58). EP with a thick apophysis carrying a tooth (*C. pallidula*, *C. ezoensis* — Fig. 55). EP-apophysis covering EB (*C. pallidula*, the *hummeli*-subgroup). E short, thick, curved, in *C. phragmitis*, *C. sapaikensis* and the *propinqua*-subgroup more or less dagger-like, directed retrolaterad and occupying 1/2-2/3 of bulb width, with a free top (Fig. 57); if E long, as in the *hummeli*-subgroup, it is directed proximad at 1/3 length of bulb and combined with a double ridge on EP-apophysis (Fig. 59). "Conductor" largely lacking, being present only in the *hummeli*-subgroup. Seminal duct long, sinuous.

Female. CO ovoid, not deep, positioned laterally near hind edge of genital plate, rarely at the edge, as in *C. langei* and *C. zyzini*, or removed from the edge, as in *C. ezoensis* and *C. mayumiae*, directed laterad and backward. CT arched laterad. SPT bipartite, first part small, elongate, lateral to the second one, large, ovoid in plane, but more often tubular and arched in lateral view, positioned closer to midline of epigyne (Fig. 48). Atrium circular or tubular, by shape similar to the smaller part of SPT. Genital plate smooth, in *C. komissarovi* protruding a little beyond epigastric furrow.

Clubiona (Clubiona) pallidula Clerck, 1757
Clubiona (Clubiona) ezoensis Hayashi, 1987
Clubiona (Clubiona) flexa Zhang et Chen, 1993
Clubiona (Clubiona) haensensis Paik, 1990
Clubiona (Clubiona) hummeli Schenkel, 1936
Clubiona (Clubiona) hwanghakensis Paik, 1990
Clubiona (Clubiona) komissarovi Mikhailov, 1992
Clubiona (Clubiona) kumadaorum Ono, 1993
Clubiona (Clubiona) langei Mikhailov, 1991
Clubiona (Clubiona) mandschurica Schenkel, 1953
Clubiona (Clubiona) mayumiae Ono, 1993
Clubiona (Clubiona) odesanensis Paik, 1990
Clubiona (Clubiona) oligerae Mikhailov, 1995
Clubiona (Clubiona) orientalis Mikhailov, 1995
Clubiona (Clubiona) phragmitis C.L. Koch, 1843
Clubiona (Clubiona) propinqua L. Koch, 1879
Clubiona (Clubiona) pseudogermanica Schenkel, 1936
Clubiona (Clubiona) sapaikensis Paik, 1990
Clubiona (Clubiona) tateyamensis Ono, 1989
Clubiona (Clubiona) venusta Paik, 1985
Clubiona (Clubiona) zacharovi Mikhailov, 1991

Clubiona (Clubiona) zyzini Mikhailov, 1995

The *hummeli*-subgroup

Diagnosis. Having a typical epigyne, the species of this subgroup differ only by male characters: E long, EP-apophysis with a double ridge, membranous "conductor" present (Fig. 59).

Description. Male. TiA with a cluster of branches, a little similar to the *obesa*-group (especially *C. flexa*). EP covering EB.

Female. See Description of the group⁶.

C. hummeli, *C. flexa*, *C. odesanensis*

The *propinqua*-subgroup

Diagnosis. The male differing by the semicircular ventral branch of TiA directed ventrad, then after curvature, dorsad (Fig. 58). Female is indistinguishable.

Description. Male. EP-apophysis and "conductor" lacking. E relatively short, not longer than 2/3 of bulb width, dagger-like, sometimes with an uneven edge (*C. propinqua*).

Female. See Description of the group.

C. propinqua, *C. mayumiae*, *C. pseudogermanica*

The *reclusa*-group

Diagnosis. The male differing by the characteristic harpoon-like ventral branch of TiA (Figs 60-61) and the presence of a tegular conductor named here protector (Fig. 7). The female differing by a short diverging CT and the considerable distance between atrium and SPT (Figs 49-50).

Description. Male. TiA divided into 2-3 branches, with a harpoon-like ventral one, in *C. bashkirica* the typical contour is visible only in lateral view. As a rule, EP carrying an apophysis with 1-2 acute teeth at top or on true conductor (lacking in *C. bashkirica*). E thin and curved, EB covered by EP (except *C. bashkirica*). Tip of E positioned near tip of protector at the distal edge of alveolus, sometimes protruding beyond its limits. In *C. bashkirica*, protector similar to the corresponding flat membranous structure in the *lutescens*-group.

Female. CO slit-like, vague, positioned at the hind edge or in the hind part (*C. bashkirica* — Fig. 50) of genital plate, rarely rounded or ovoid, situated in the middle part of genital plate (*C. maracandica*, *C. rybini*). CT short, directed laterad. SPT consisting of two reniform parts (a different shape in *C. bashkirica*). Atrium removed from SPT, located near hind edge of genital plate (Figs 49-50). Atrio-spermathecal tube long, directed to the median line of epigyne. Genital plate mostly wrinkled, usually covered by hairs.

Clubiona (Clubiona) reclusa O. Pickard-Cambridge, 1863
Clubiona (Clubiona) bashkirica Mikhailov, 1992
Clubiona (Clubiona) californica Fox, 1938
Clubiona (Clubiona) canadensis Emerton, 1890
Clubiona (Clubiona) evoronensis Mikhailov, 1995
Clubiona (Clubiona) interjecta L. Koch, 1879
Clubiona (Clubiona) kulczynskii Lessert, 1905
Clubiona (Clubiona) maracandica Kroneberg, 1875
Clubiona (Clubiona) norvegica Strand, 1900
Clubiona (Clubiona) pacifica Banks, 1896
Clubiona (Clubiona) rosserae Locket et Millidge, 1953
Clubiona (Clubiona) rybini Mikhailov, 1992
Clubiona (Clubiona) saurica Mikhailov, 1992
Clubiona (Clubiona) stagnatilis Kulczyński, 1897
Clubiona (Clubiona) subsultans Thorell, 1875

⁶The epigyne of *C. flexa* is very similar to *C. wolchongensis* in the *latericia*-subgroup of the *obesa*-group.

The *caerulescens*-group

Diagnosis. The male differing by the strong development of divided TiA and the free E without any conductor and EP-apophysis (Fig. 62). The female differing by the epigyne hanging far over the epigastric furrow and strongly sclerotized at its hind edge (Fig. 51).

Description. Male. TiA strong, with three branches, the middle one bifurcate at top. E beginning in proximal half of bulb, very long, directed distad, then angled around tegulum and moving on proximo-laterodistad.

Female. CT directed forward, being parallel to each other at midway. SPT simple, bordering an ovoid atrium. Ca. 2/5 of epigyne length located beyond epigastric furrow.

Sclerotization of the hind part of the genital plate seems to correspond to the large size of the male TiA.

Clubiona (Clubiona) caerulescens L.Koch, 1866

The *chabarovi*-group

Diagnosis. The male differing by TiA strong but weakly sclerotized (Fig. 63), the female by the weakly sclerotized epigyne hanging over the epigastric furrow, with large depressions in the fore part being directed forward (Fig. 62).

Description. Male. TiA strongly depressed inward and convex outward, so it can be considered as a hollow structure. It consists of two unequal branches. EP-apophysis covering EB. E directed distad, protruding beyond limits of alveolum.

Female. CO opening in a groove at hind part of genital plate, latter hanging back over epigastric furrow. CT directed forward, being parallel to each other in the middle part. SPT simple. Huge, weakly-sclerotized, paired depressions in the fore part of genital plate corresponding to large male TiA.

Clubiona (Clubiona) chabarovi Mikhailov, 1991

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