the impact of predators were also emphasized by Pijanowska [1990, 1992] but without specifying the relative influence of each type of predator.

Certainly, the above is only one of the possible explanations. Seasonal morphological transformations may be of more complex nature. According to Ellev [1985], the enlarged helmet and spine in D. retrospect failed to prevent the rate of the consumption by Chydorus and Leptestina. Accessory morphological structures in zooplankters first of all perform protective functions, and as such they could have acquired as adaptations to life in open water [Pijanowska, 1990; Fryer, 1991].

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6. References

ABSTRACT: By means of a newly rediscovered typological approach in the spider genus 
Clubiona, here restricted solely to the scope of the Holartic fauna, four subgenera are distinguished, with 15 species groups and 10 subgroups distinct in the subgenus Clubiona s.l. alone. A thorough analysis of all morphological diagnostic characters of the species representing various species groups, subgroups, and subgenera is provided. The taxon a rank in typology is the level of generalism of the taxon a rank. Ordering of the subtaxonomic groupings which are significant for the modern world, and one and three main and one and three morphological type, with mostly conjugated characters of male and female genitalia underlying each infrageneric grouping.

REZON: Pri pomoci typologicheskogo metoda v sostave roda Clubiona (v obrasse \l",kaevochnoi kafedri) vydeleno 4 podroda, a v podrodde Clubiona s.l. 15 morph and 10 podgruppeg. O vgorochykh zoon 3 otnishnih i o osobennih karakterakh bi haraktera shts"khoj kategorii. V to"m, o"to, podroda diffrerii"tya bo"s driv o"deh roda (ocharatera) shts"khoj kategorii.

In particular, typology is used below for the separation of infrageneric groupings routinely treated as quite obscure commonness often confused 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 Holartic fauna, besides those groupings established earlier, with the addition of new species recently discovered in the Oriental realm [Mikhailov, 1990, 1991, 1994]. At present all of these groupings have been accepted in the arachnological literature [e.g. Oso, 1992; Hayashi & Yoshida, 1993], yet the ground 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 for reciprocal illumination — cf. Henning, 1979: 21.

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 derived from Japan, Korea, and China.

The following abbreviations are accepted below: CO - copulatory openings, CT - conjunctival tubes, E - embolus, EB - embolar base, EP - embolar part, SPT(G) - spermatocele(s), 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 meronomic level. Thus, leg armature and reciprocal ratios of leg articles provide a safe recognition of the genera *Clubiona*, *Elatior*, and *Cheiracanthium*. In some cases, the pattern of dorsal abdominal coloration promotes species identification, e.g. *C. japonica*, *C. jucunda*, *C. riparia*, *C. subtilis*. 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 *Mittigidae* (N. Platnick, personal communication). The problem of the upper taxonomical level 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 [Lyybarsky, 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 bioprocess concept. Evolution of the Order Araneae is generally considered to be associated with the development of spinning activity 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, the principal part of the palpus, 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, 1985: 154; Kraus, 1984; Cordungton, 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

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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.
Paraclubiona: C. ny,u,na, neHTpahbHo, morphotype. sclerotized in part. TI A weakly developed. Rarely only enlargement of male copulatory organs can be described as follows: hammer-like outgrowth (Figs 6-7). This species is entered in the bulk of species diversity of the genus (about 30). It arises at the tegulum normal, tegumen normal, and the direction of the epigynal tubes, both more generalized than 1b + 1, CO in the hind part or at the hind edge of the epigyne. CT directed straight forwards.

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

Besides the subgeneric level, certain structural peculiarities of the male (EP and TP) and female (CO, CT, atria, SPTE) allow to separate groupings of yet another, lower, level traditionally allotted in arachnology the rank of species-groups, this time of the no nomenclatorial status. Such an extra-nomenclatorial division 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 61]. 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, 1985]. In several spider taxa, for example, Micaria (Greek), 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 infraspecifically, i.e. lower than at the species level. Intraspecifically, i.e. between species within species-groups, they vary much more considerably.
The subgenus Paracubiona includes only one species-group, which formally can be named the corticis-group. This statement is quite preliminary, since numerous species from Southeast Asia and Australia require a modern revision.

Japaniona comprises one group, whereas Buciana is represented by a single species only.

By the conjugation criterion, the following groups are distinguishable within Cubiona 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 22, 23); the lutescens-group: a flat TiA combined with a wide E; a simple structure of a circular SPT (Figs 8-10); the laetia-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 E ("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. 12).

The chabareci-group: stereospecificity of a characteristic TiA and the epigynal depressions disposed separately from CO (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 akaginis-group, or curved spirally, as in C. kimyongnii (Fig. 26). Sinuous CT of the female is 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 basically 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 polychetical characters (Table 1; e.g. 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 essentially by the male palisade 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. bakurani (the oesma-group), displaying no fundamental differences from the set of diagnostic features of the latter group.

Thus, the separation of 10-11 species-groups...
Infrageneric groupings within the spider genus Clubiona


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

able 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 breviseta-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 sub-
groups, as shown below for the obesa-group.

At the moment, subdivision of all Clubiona s.str. into species-groups seems impossible, since the exact morphological description of some species is unknown. Moreover, it may be caused by purely morphological reasons, as in the linyphiid genus Lepthyphantes [Tunasevitch, 1902].

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 generalization of diagnostic characters is shown in three species groups, i.e. there are only little differences between species inside such subgroups. Thus, in the propinqui groups (all species included, C. propinqua, C. pseudoemoronica and C. majunam), which are almost identical in Tia structure (Fig. 22, Table 1), they remain also basically unknown in other Clubiona. Differences between these species lie in body size (with a considerable interspecific variability), (C. propinqua - all others - in both cases - Figs 56, 57), and direction of the seminal duct inside EP (C. pseudoemoronica has the seminal duct directed forwards, whereas C. majunam - directed backwards). Female distinguishing features are also very slight. Similarly, the genaeven- subgroup (comata-group) (Figs 20, 21) can be characterized by the presence or absence of differences in the uniformly general structure of the male palpi and endopods.

Besides that, a lot of groups have reasonably long been established within the oseus-group. The latter is quite species-rich and differs only 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 oseus-group that display highly disjunct and ste- reoisopically arranged genitalia. Thus, C. bakarurki and C. iritm also belong in species-subgroups of their own. All other than other subgroups can be established within the Palaearctic obscura- group: the ahateniensis- (Japan), the latericius-, the melanosticta-, the pseudoemoronica- and the iritm-subgroups (for the geographical distribution of the last five of these, see Mikhailov, 1992).

A list of all subgroups and species-groups seems impossible due to morphological reasons.

Establishment of three levels of infrageneric groupings (species-group - species-subgroup - species) is undertaken here for ordination both of generalism and the extent of morphological differ- ences. 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- na species. In this group, the genus Clubiona and C. micans are often very alike (except C. lycosella), C. hainana and C. manica being highly dynamically archetypal. Separation of some smaller subgroups within the Clubiona seems to be useful there from a purely generalisational viewpoint.

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C. than that in the male genitalia. Being surrounded from three sides by the palpi, the shape of its tube can be only circular, oval, or tubular. Whereas the growing capacities of the male bulb are far less extensive, the male epigyne differs considerably more in size than atrium and situated near its back part or almost equal in size to atrium and situated near its back part (C. trissialis (CT), C. subtrivialis). C. japonica (L.Koch, 1878) C. (Clubiona) vigil Koch, 1879


Type species: Clubiona juncunda (Karsch, 1879). Diagnosis. The male differing by the singular position of E mostly lying between the bulb and the cymbium (Fig. 53). The female differing from that of Parclubiona and Japoniona by E placed caudally and CT directed forwards (Fig. 14). Description. Male TIA short, not branched. Tegular apophysis rectangular, not unform. Tegular conductor filiform. Female. A large genital groove in hind part of epigyne. CT directed forwards, sinon SPT large, tegular CT (Clubiona) juncunda (Karsch, 1879)

Subgenus Clubionus sensu stricto.

Type species: Clubiona pallidula (Clerck, 1757). Diagnosis. The male differing by the conductor of embolar nature combined with the sclerotized tegular apophysis. Tegular apophysis not separated from epigastric furrow, CT and E lying near the rear of the epigyne as well as CT directed forwards. Description. Male. TIA usually well-developed and sclerotized, often of a complex shape. Bulb usually elongated, conductor not always expressed. E of variable shape, from aciculiform and aciculiform to oblong- limiform, directed retrodorsal or proximal, sufficiently long. Female. CT more often long. Atrium sclerotized, usually placed in SPT, CT directed forwards, circular or tubular, sometimes bipartite and strongly curved sagittally.

The trissialis-group

Infrageneric Diagnoses. 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 structure of circular or oval SPT combined with CT directed togethe or fused into a single groove, and CT straight or almost straight (Fig. 15). Description. Male. TIA as in Diagnosis, tendency to enlarge in C. rostrata and C. transbaicalica. EP with small apophysis near EB, sometimes bearing 1-3 teeth. EB covered by EP-apophysis (except C. lycosella). E placed totally in apical part of bulb, arched around or angled across tegular tip, sometimes stretching proximal along a margin of EP, or partially directed to the side of the tegular C. trissialis (C. rostrata). Seminal duct relative long, C. rostrata long.

Female. Hind edge of epigyne usually projecting a little beyond epigynial furrow (except C. boskii). CT small or even without epigyne, fused as latter to top. Bulb non-protruding. Conductor tegular, consider- ably larger than E, weakly sclerotized, of a characteristic shape. Tegular apophysis of a characteristic shape hooked or bent, with anterior or lateral margin of tegular CT enlarged.
developed, flat, wide TiA and embolus conductor (Fig. 6). The female differing by CO widely separated from each other combined with CT almost straight and the epigynal duct diverging. Description. Male. TiA containing ca. 0.4-0.5 of cystil.

The maritima-group

Diagnosis. Male. EP with a large sper-los-like apophysis protruding beyond cystilum (Fig. 23). Female. CO slit-like, circular, sper-los/epicone adjacented, hind edge of epigyne strongly sclerotized (Fig. 4B). Description. Male. TiA with three branches, each not longer than 1/3 of the cystilum length. Epigynal duct converging to EB. E long, arched around bulb tip, then stretching proximally along a membranous "conductor." Female. In Diagnosis. CT thin, long, first diverged, then converged. 

The breces-group

Diagnosis. Male differing by the characteristic bifurcate epophysis (Figs 24, 32). Female by CT diverging from middle to be combined with the simple cystilum SPT (Fig. 18). Female. Known only in C. breces. CO fused into genital groove of a characteristic multifarious shape. CT diverging. CO then curved forward. At the bulb a little longer than SPT, bordering spt unipartite. Circular. The group includes the subgroup diagnoses. 

The comta-group

Diagnosis. Male differing by the bifurcate convex and non-furcate TiA as well as by a dark spot of thick hairs on the prolateral side of the cystilum (Fig. 26). The female differing by the male genital groove characteristically semi-circular or inverted coroidum (Fig. 20). Description of both male and female coincides with the group description including the subgroup diagnoses. 

The lutescens-group

Diagnosis. Male differing by the bifurcate convex TiA (Fig. 28) combined with the vibran atrium and tubular, unipartite SPT curved from the depth of the vulva (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 from the middle of the vulva, directed prolaterad, then arched around bulb tip and moving on retrolaterad along alveolar wall, some times coiling at bulb tip; often with a thin crest.

The japonica-group

Diagnosis. By the structure of the male genitilia, the group is close to the similis-group. Ep-apophysis converging by the thin E or more than thin TiA (Fig. 30). By the structure of the female genitalia, it is close to the similis-group, distinguished by the circular SPTae (Fig. 30).

The zilla-group

Diagnosis. Male differing by the large branched E apophysis without wider bulb (Fig. 31). Female differing by the presence of a transverse furrow with slit-like CO at its corners (Fig. 39).

The similis-group

Diagnosis. The male differing by the weakly convex, branched E apophysis with a ventral branch more than thin, narrow and attenuating, combined with a thin E (Fig. 29) and the absence of "conductor." Female differing by CO long, strongly curved in distal half, combined with the simple oval or tubular SPT not curved in the depth of the vulva (Fig. 22).

The thecatus-group

Diagnosis. Male. TiA bifurcate, with the ventral branch either thin (C. similis, C. neglecta, C. adusta, C. pseudosaxatilis) or arachnico-genital (C. congruens, C. congestilis). EB apparently fused with EP-apophysis. E thin, arising from the middle or distal part of bulb, diverging forward or strongly curved across the upper half in most species, so that all surface returning to EB in C. neglecta.

The similis-group

Diagnosis. Male. TiA headed of epigyne, sometimes in groove in epigyne hind part (C. pseudosaxatilis, C. congestilis). CT wide, directed parallel forward or slightly diverging (Fig. 22). Sometimes in groove in epigyne hind part, coiling several times in middle part of vulva, converging toward midline and finally a little diverging. Atrium circular and oval, placed in front of SPT and then more laterally. SPT simple, oval, sometimes considerably less in size than atrium (C. pseudosaxatilis) or cowly circular (C. pseudoscutata), rarely tubular (C. similis). Epigynal surface smooth.

The obesa-group

Diagnosis. The male differing by the wide TiA usually convex ventrally and concave dorsally (Figs 32-33, 35-36). Sometimes with a little strongly developed. E thin, usually supplied with a membranous "conductor" on tegular surface. Female differing by CO long, strongly curved in distal half, combined with the simple oval or tubular SPT not curved in the depth of the vulva (Fig. 22).

The obesa-group

Diagnosis. Male. TiA differing by the shape of the male genitalia, the group described including the subgroup diagnoses. 

The similis-group

Diagnosis. The male differing by the weakly convex, branched E apophysis with a ventral branch more than thin, narrow and attenuating, combined with a thin E (Fig. 29) and the absence of "conductor." Female differing by CO long, strongly curved in distal half, combined with the simple oval or tubular SPT not curved in the depth of the vulva (Fig. 22).

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Diagnosis. The male differing by the wide TiA usually convex ventrally and concave dorsally (Figs 32-33, 35-36). Sometimes with a little strongly developed. E thin, usually supplied with a membranous "conductor" on tegular surface. Female differing by CO long, strongly curved in distal half, combined with the simple oval or tubular SPT not curved in the depth of the vulva (Fig. 22).
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The sapporensi-subgroup

Diagnosis. The male differing by the presence of one (ventral) branch of TiA turned typically for the total group, the short E, especially directed upwards, and the long CT, some-developed in the hind part of the leg (Fig. 44). Female. CO small, rounded (C. chikuni, C. haeinsensis, C. tsuraki, C. wakimani, C. phragmitoides).

The sapporensi-subgroup

Diagnosis. The male differing by the short E, not wider than TiA, and strongly deformed at the distal part (Fig. 44). Female. CO small, rounded (C. chikuni, C. haeinsensis, C. tsuraki, C. wakimani, C. phragmitoides).

The sapporensi-subgroup

Diagnosis. The male differing by the tip of TiA curved downwards, combined with the depression in the genital plate serving as part of the adventitious structure. Female. CO small, rounded (C. chikuni, C. haeinsensis, C. tsuraki, C. wakimani, C. phragmitoides).

The sapporensi-subgroup

Diagnosis. The male differing by the presence of one (ventral) branch of TiA turned typically for the total group, the short E, especially directed upwards, and the long CT, some-developed in the hind part of the leg (Fig. 44). Female. CO small, rounded (C. chikuni, C. haeinsensis, C. tsuraki, C. wakimani, C. phragmitoides).
The caerulescens-group

Diagnosis. The male differing by the strong development of divided TiA and the free E without any conductor and the male epigynum strongly sclerotized at its hind edge (Fig. 51).

Description. Miura (1982, p. 169) describes the epigyne hanging far over the epigastric furrow and half of bulb, very long, directed distad, then arched with large depressions in the fore part being directed and convex outward, so it can be considered as a hollow corresponding to large stepeni kandidata biologicheskikh nauk. Moscow: MGU Publ. 21.


