

Why no subspecies in spiders?

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Abstract

The several tens of thousands of spider species that have been named so far have almost exclusively proved to be morphospecies; some of them have been tested and proved to be biospecies, but subspecies have only been recognized in a few exceptional instances. This phenomenon cannot be explained by regular speciation mechanisms alone: obviously, these are no different from those occurring in other groups of the animal kingdom. However, the species groups that have been sufficiently investigated in spiders indicate that separation fairly quickly produces superspecies composed of allospecies ('semispecies'). The origin of allospecies patterns can be explained by a combination of the regular effects of separation with functional needs to safeguard sperm transfer between sexual partners. Selection pressure towards optimal co-adaptation between male and female copulatory organs may shorten transitory phases at a subspecies level. This could explain the origin of superspecies composed of similar but clearly distinguishable biospecies (allospecies); primarily, they are unable to coexist sympatrically or even syntopically.

Key words: Arachnida, Araneae, speciation, genital coadaptation, superspecies, allospecies

INTRODUCTION

It was Ted Locket who raised the critical question of whether some linyphiid spiders from remote localities in Europe really represented true species, as there were only slight morphological character differences on which to base this decision. This was almost 25 years ago on the occasion of the 7th International Congress of Arachnology held in Exeter. His preliminary remarks did not form part of the congress volume (see Merrett 1978), but the problem was of course not forgotten by systematists, who were interested in the general aspects of speciation and evolutionary biology. However, I am not aware of any sound discussion later. Not even a hypothesis has been published. So far, spider taxonomists have stamped tens of thousands of morphospecies, but subspecies have

only been named in exceptional instances. It may be questionable as to whether such nominal taxa really form subspecies, i.e. subunits of polytypic species. The aim of the present contribution is to stimulate discussion by investigating this comparatively unusual situation in more detail. Of course, tradition has played and is continuing to play a predominant role, i.e. the stabilizing effect of long-established taxonomic practice. However, the real biological situation may not be reflected by practicing conventional procedures of this kind. There is accordingly a real need to try to explain why there is practically no problem in distinguishing morphospecies from morphospecies without any intermediate forms. This aspect is directly linked to modes of speciation in spiders.

GENERAL REMARKS ON SPECIES AND SPECIATION

The investigation and subsequent attempts to explain this situation will first need some general remarks.

Allopatric versus sympatric speciation

Allopatric speciation is the predominant mode of speciation in animals. Separation by barriers causes interruption of genetic exchange between groups of populations; peripheral isolates especially play a major role. Accordingly, interruption of the coherent function of gene flow permits divergence (see Mayr 1942, 1963). Sympatric speciation, i.e. speciation without geographic isolation, cannot be definitively excluded, but there is no reason to believe that mechanisms of this kind could be of major importance.

Until now, no sound argument has been put forward to contradict this general view.

Polytypic and monotypic species

In most sufficiently studied major groups of the animal kingdom, many biospecies¹ comprise two or more subspecies. As defined by Mayr (1963), subspecies form an 'aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species'. Numerous examples are well-documented from mammals to birds and from lizards to salamanders, etc. This is also true for invertebrates such as carabid beetles (Mossakowski & Weber 1976), and pulmonate gastropods (Knipper 1939; Mayr & Rosen 1956). See Mayr (1963) for details and further documentation.

According to this definition, the subdivision of polytypic species into subspecies is based on typology. This explains why, in a given species, different numbers of subspecies have occasion-

ally been distinguished by different authors. Polytypic species seem to occur almost universally (Rensch 1929).

The counterpart - monotypic species - seems to be exceptional. This term designates species without subspecies. They may be geographically widely distributed. I refer to the holarctic distribution of the araneid *Araneus diadematus* Clerck, 1757 (Fig. 1) and similar distribution patterns of various species of the Erigonidae. Could it be that species of this kind consist of just one single panmictic population? If so, they may be barred from geographic speciation. The same seems to be true for freshwater Bryozoa and various species of the Tardigrada, e.g., *Macrobiotus hufelandi* C.A.S. Schultze, 1834 but there is evidence now that this tardigrad species is composite (Bertolani & Rebecchi 1993). These and other cases have in common the trait that the species concerned share extraordinary dispersal abilities. I refer to ballooning in spiders, to blepharoblasts in freshwater bryozoans and to the desiccated cryptobiotic states in tardigrades.

ANALYSIS

The situation in spiders is heterogeneous. There are sedentary species, and in the other extreme, others are world champions in ballooning like the Tetragnathidae in the Northern Hemisphere. Species may have extremely wide holarctic or pantropic distribution patterns, such as *Neoscona nauticus* (L. Koch, 1875). Others are confined to relatively small areas (see, for example, Thaler's work on alpine species (1994; Thaler et al. 1994)).

Almost all these species have in common the fact that they are distinct morphospecies. There is practically no variation. This is especially true for the taxonomically decisive genital structures. Examples of the narrow limits for variation of such details are presented in Figs. 9-10; they are partly correlated with the occurrence of separated populations (see Kraus & Kraus 1988). Intermediate populations or at least single intermediate specimens between different morphospecies are almost unknown in nature² — with the exception of extremely rare teratological individuals. There is usually no difficulty in

¹The present author continues to accept the biospecies concept sensu Mayr (1963) as it is biological. What is called the phylogenetic species concept does not seem to be applicable in the present discussion: it is based on individuals, not classes, and sets of characters (Goldstein & DeSalle 2000), i.e. close to typology.

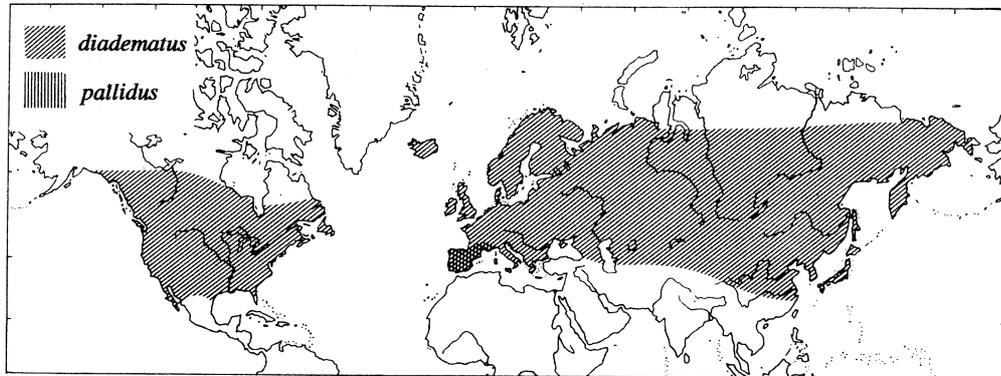


Fig. 1. Holarctic distribution of *Araneus diadematus* and limited distribution of its presumed sister species, *A. pallidus* (from Grasshoff 1968).

assigning even single specimens to morphospecies A, B, or C.

It is highly improbable that the modes of speciation in spiders could be principally different from those in other animals or at least in other groups of terrestrial arthropods. For better understanding, three aspects should be considered:

1. Arguments in favor of regular allopatric speciation mechanisms

Various cases are wellknown enough to provide information on speciation events caused by geographical separation. Some selected examples are:

Mesothelae

Species differentiation in island representatives

²Hybrids between *Tegenaria gigantea* Chamberlin & Ivie, 1935 and *T. saeva* Blackwall, 1844 were found in Yorkshire, England, where both species occur sympatrically (Oxford & Smith 1987; Oxford & Plowman 1991). Only 3% of the sampled male specimens were identified as intermediates. They occur occasionally; no hybrid populations were found. Hence, the specific status of the two *Tegenaria* species is not invalidated. There is evidence that two closely related synanthropic species are expanding their ranges, perhaps caused by human interference (see Mayr 1963). This case does not seem to be of any relevance for the present discussion.

of the genus *Heptathela* and closely related forms (*Ryuthela*) studied by Haupt (1983) indicates a correlation with their separation on different islands (Fig. 2). With respect to only slight differences between material of different origins, Haupt divided *H. kimurai* (Kishida, 1920) into the nominate and three further subspecies, and

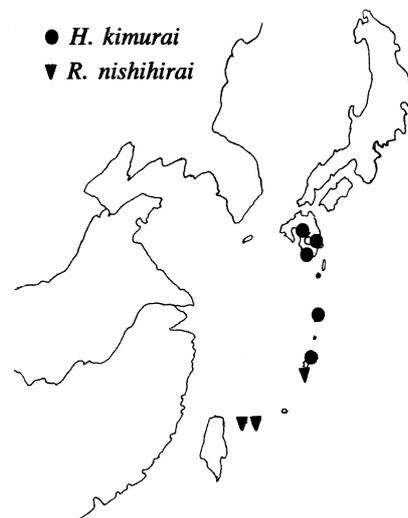


Fig. 2. Distribution pattern of island representatives of the genera *Heptathela* and *Ryuthela* on southern Japanese islands. Further differentiation into presumed subspecies (*H. k. kimurai*, *k. amamiensis*, *k. higoensis*, *k. yanbaruensis* and *R. n. nishirai*, *n. ishigakiensis*) not indicated (from Haupt 1983).

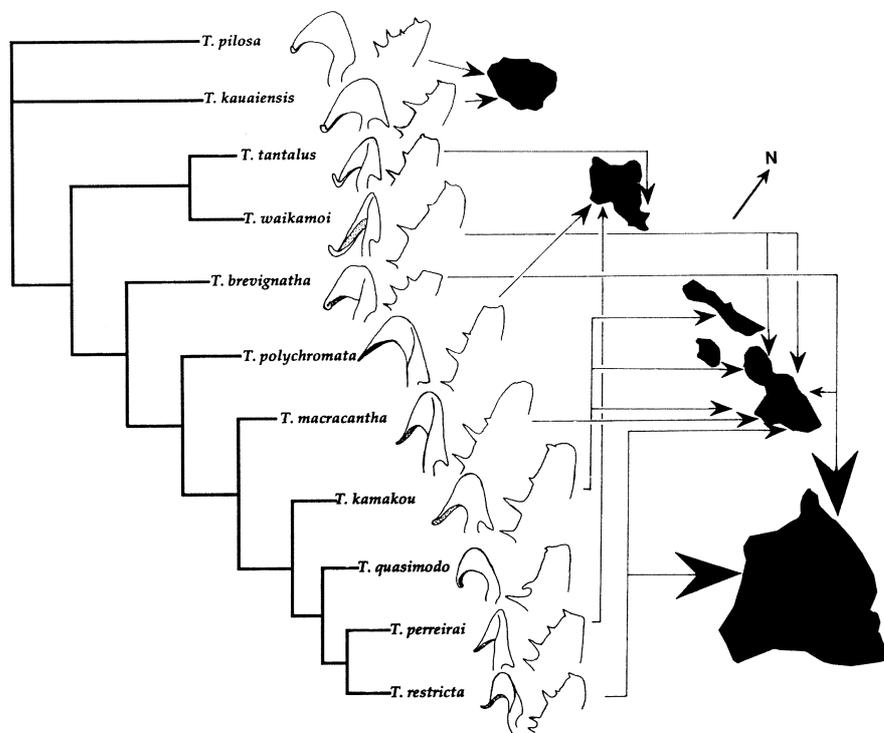


Fig. 3. Phylogenetic biogeography of a clade of Hawaiian *Tetragnatha* species (from Gillespie 1993); (distribution of the widely distributed species *T. quasimodo* [Hawaii, Maui, Molokai, Lanai, Oahu, Kauai] not indicated).

R. nishihirai Haupt, 1979 [= *Heptathela* ?] into the nominate and one subspecies. Because of the discontinuous distribution of the species, especially those occurring on islands, it is hard to decide whether these phenons form part of two polytypic species or whether differentiation into biospecies has already been achieved.

Anyway, the *Heptathela* case is a convincing case of allopatric differentiation.

Colonization and differentiation in the Hawaiian Archipelago

In her extensive work on Hawaiian spiders, Gillespie (e.g. 1993; see also Roderick & Gillespie 1998) investigated the radiation of certain spider groups, especially tetragnathids. She discovered a fascinating example of differentiation and speciation (Fig. 3). Among others, there is one clade of cursorial hunters, with the typical

web-building behavior totally reduced. Gillespie concluded that multiple founder events occurred and that speciation required strict geographic isolation; ecological (more than sexual) shifts appear to play a role in initiating divergence. In principle, but not exclusively, islands were primarily colonized in the sequence of their age, i.e., from north to south. Multiple invasions may have happened, and present distribution patterns indicate cross-colonizations. This development parallels the diversification of the Hawaiian Drosophilidae into more than 500 species, approximately 98% of them endemic (for a review see White 1978).

The conclusion is that even tetragnathids can be subject to complex allopatric speciation events. Their diversity on the Hawaiian islands apparently forms a typical case of archipelago speciation (Mayr 1963); together with various other

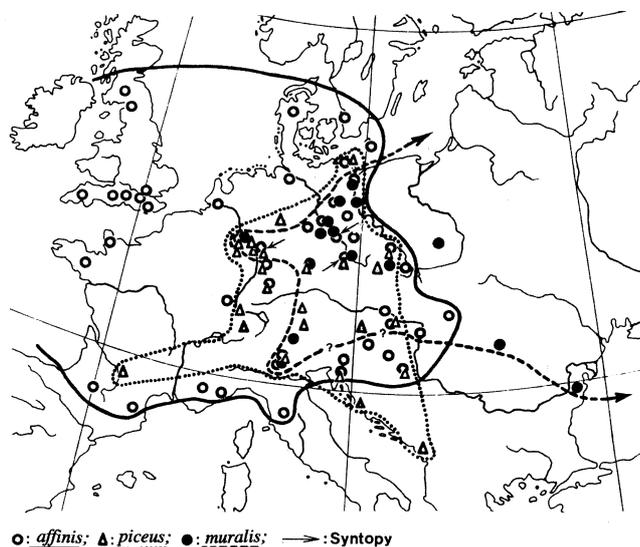


Fig. 4. Distribution of *Atypus* species in the western Palearctic Region (from Kraus & Baur 1974).

examples, it is more spectacular than the well-known radiation of Darwin's finches in the Galapagos archipelago (see also Wagner & Funk 1995).

Atypus species in the western Palearctic Region (*Atypidae*).

Three *Atypus* species occur in the western Palearctic Region (Kraus & Baur 1974)³. Their differentiation is obviously correlated with Pleistocene separation into habitats in Western Europe, southern Siberia, and a southeastern refugium in the Balkan region (Fig. 4). Corresponding to these refugia, the recolonization of Central Europe apparently occurred from three directions [for principles of reasoning see de Lattin 1967]. There is no reason to doubt that the three species originated by allopatric speciation; they prove to be biospecies as localities are known where they coexist sympatrically; hybrids were never found.

Heriaeus species in the western Palearctic Region (*Thomisidae*).

Loerbroks (1983) revised the species of the

thomisid genus *Heriaeus* of the Western Palearctic. He distinguished three species groups and mapped the distribution of 11 species of the *H. hirtus* group (Fig. 5). This distribution pattern may be explained by referring to various well-known glacial refugia. They are currently designated as Adriato-mediterranean (plus tyrrhenian), ponto-mediterranean, Syrian and Mauretaniens faunal elements (see de Lattin 1967). They recolonized Central Europe. This is another example of regular allopatric speciation.

One could continue, but this would lead to redundancies. The conclusion is that there is no evidence at all for assuming special modes of speciation in spiders. But this kind of review does not provide an answer to the central question: why were all of the tens of thousands of spider species described almost exclusively as monotypic units?

2. Extremely wide distributional areas versus patterns of local species

As already mentioned, there is a wide spectrum between holarctic and also pantropic distributional patterns, on the one hand, and considerably small areas of occurrence on the other.

³There is evidence that *Atypus muralis* Bertkau, 1890 is not different from *A. karschi* Dönitz, 1887 (see Kraus & Baur 1974).

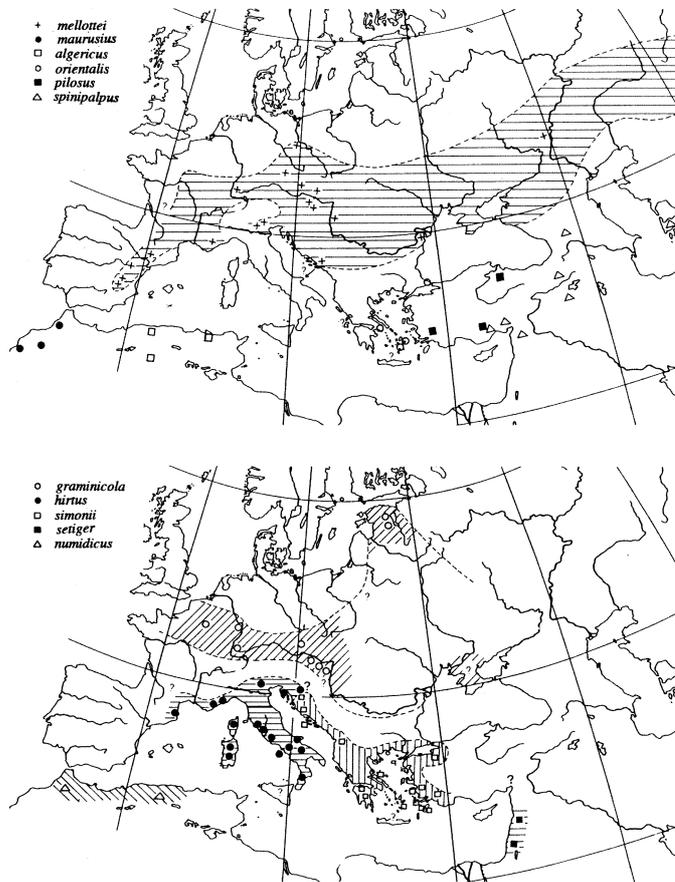


Fig. 5. Distribution of species of the *Heriaeus hirtus* group in the western Palearctic Region (from Loerbroks 1983).

Geographically wide distributional areas

It is difficult to explain why certain species were extremely successful in extending their range, cosmopolitan areas included. The impression is that they form one single panmictic population in certain instances. This can be assumed, e.g. in the case of *Araneus diadematus*, as ballooning spiderlings may rotate eastwards because of the prevailing wind direction in the Northern Hemisphere. Grasshoff (1968) stated that specimens of *A. diadematus* from Japan or from North America cannot be distinguished from their European conspecifics. Various ecophenotypes, color variants included, occur repeatedly at different localities. However, there is no discernible difference at all in the complicated genital structures. Uhl et al. (1992) made a similar observation in their study on the North American species *Tet-*

ragnatha shoshone Levi, 1981, then newly discovered in Europe. As the differences on both sides of the Atlantic proved to be gradual, not even subspecific rank was assigned.

Geographically limited distributional areas

Some presently limited distributional areas may be relics of formerly wider distributions, but it seems to be much more probable that most of them are the result of speciation events caused by complex separations. Glaciations in the European Alps form a good example (for review see de Lattin 1967). There was a complicated pattern of relatively small 'Nunatakker' and also of major refugia ('massifs de refuge'). This kind of fragmentation of previously coherent distributions may well have induced allopatric differentiations, including speciation. Attempts to link

separations in the past (in refugia) of this kind with geographically limited recent distribution patterns of spiders may — but must not — be speculative.

Despite the fact that no reliable method is known for measuring dispersal ability, spiders should not be underestimated. Wunderlich, for instance, collected thousands of individuals of spider species in a limited area in Berlin. Among others, he also found one single male specimen of the hitherto unknown species *Entelecara berlinensis* (Wunderlich, 1969). As in birds, it could well be that this was nothing other than an accidental occurrence - as a result of dispersal ability and different from the existence of an established reproducing population. The same is true for the discovery of one single female of *Araneus grossus* (C.L. Koch, 1847) in south-western Germany. The species was reported by Wiehle (1963) as 'new' for Germany; but until now, no further specimen has been found. This demonstrates that occurrence due to dispersal ability should be distinguished from the existence of firmly established, reproducing populations.

The conclusion is that the extension of distributional areas does not depend on dispersal ability alone. Abiotic factors (such as climatic conditions), narrow specialization in biological properties, the ability to form an ecological niche within the framework of complex interdependencies (including competition with other, already well-established species) may effectively prevent the extension of geographically limited distributions. Situations cannot be excluded in which closely related species occur allopatrically, as they lack sufficient mutual differentiation. This may explain why allopatry in species with limited distributions could be obligatory.

Similar situations of mutual exclusion have already been found in other animal groups, including even mammals. As an example, I refer to species of the coccinellid beetle genus *Chilocorus* with obligatory allopatric species complexes, both in North America and in the Palearctic (see White 1978 for review and other cases). There are differences in the karyotypes, but this aspect does not seem to have been con-

sidered so far in allopatric spider species complexes. Future work in this direction could be promising.

3. No transition zones, not even hybrid belts ?

The most crucial problem mentioned at the very beginning of this contribution remains: Until now, there has been no reliable information on potential transition zones or at least hybrid belts between allopatric phena traditionally classified as morphospecies. The probability is high that intermediates of this kind do not exist at all (but see footnote 2). Genital differences may be minute, but they are always distinct in such allopatric forms, including presumably isolated populations. This is true for Mediterranean species of the genus *Amaurobius*, for representatives of the linyphiid genera *Lepthyphantes* (see Thaler 1994) and *Agyneta* (see Tanasevitch 1999), but also for *Theridion* (Theridiidae) and *Acantholycosa* (Lycosidae) morphospecies (Thaler, in litt.).

HYPOTHESIS

The present analysis demonstrates normality: Compared with other higher animal taxa, modes of speciation in spiders, as well as available biogeographical data, do not offer any exclusive features. However, there is no peculiarity discernible that could explain the traditional morphospecies by morphospecies situation in spiders. Are there still other, different aspects that should be taken into consideration?

Application of the superspecies concept

Superspecies patterns

I would like to refer to the superspecies concept first proposed by Mayr (1931). The definition given by Mayr & Ashlock (1991: 430) reads as follows: 'A monophyletic group of closely related and entirely or largely allopatric species that are too distinct to be included in a single species or that demonstrate their reproductive isolation in a zone of contact.' This corresponds exactly to the situation in very similar but allopatric morphospecies in spiders. The subunits of superspecies were called 'semispecies'. This term could be misleading, as one could conclude

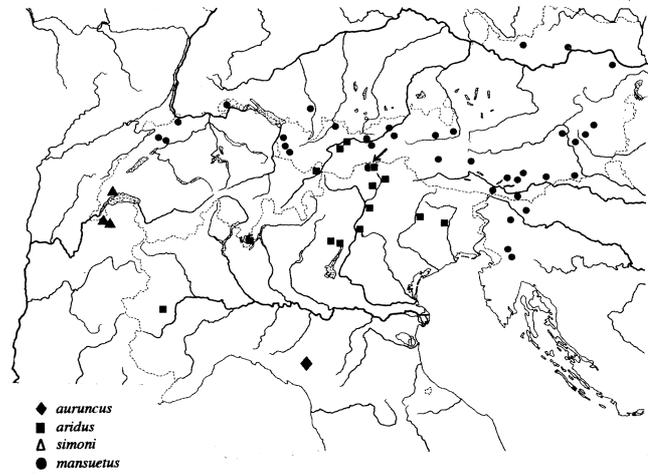


Fig. 6. Distribution of species of the *Lephyphantes mansuetus* group [= *Mansuphantes* Saaristo & Tanasevitch, 1996] in the European Alps; arrow indicates syntopic occurrence (from Thaler 1994).

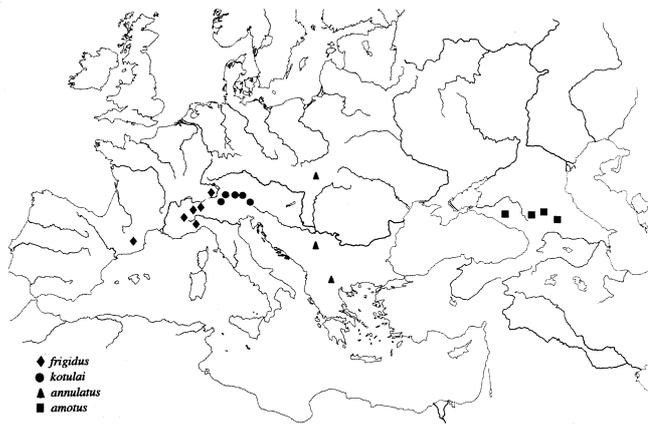


Fig. 7. Distribution of species of the *Lephyphantes annulatus* group [= *Incestophantes* Tanasevitch, 1992] in the western Palearctic Region (from Thaler et al. 1994).

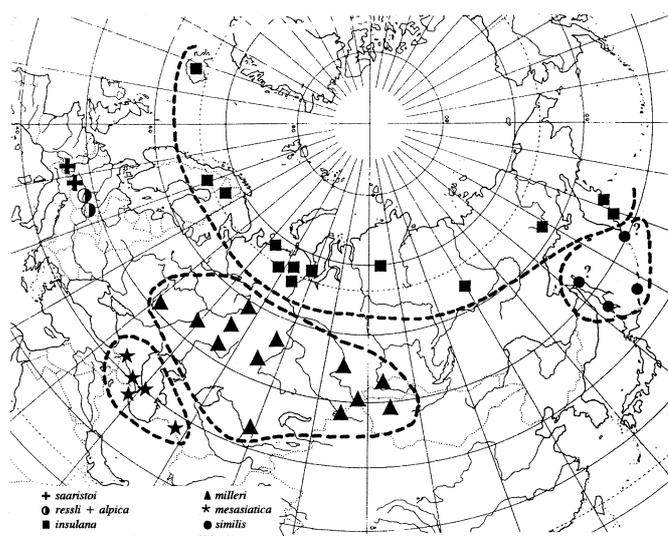


Fig. 8. Distribution of the Palearctic species of the *Agyneta similis* group (from Tanasevitch 1999).

that full biospecies rank has not yet been achieved. Thus, Amadon (1967) replaced 'semispecies' by introducing the more appropriate term 'allospecies'.

It seems to be easy to group a lot of spider phena — currently classified as morphospecies — in complexes of superspecies. The impression is that polytypic species structures (with a certain number of more or less intergrading subspecies) are replaced by superspecies, with allospecies as subunits. Well-documented examples are already known.

One could refer to the already mentioned *Heriaeus hirtus* complex (Loerbroks 1983) in thomisids (Fig. 5). The linyphiid species *Lepthyphantes mansuetus* (Thorell, 1875) and its relatives (Fig. 6) were recently studied by Thaler (1994). Thaler et al. (1994) investigated the complex around *L. annulatus* (Kulczynski, 1882) (Fig. 7). Similar results were obtained by Tanasevitch (1999) who investigated *Agyneta* species (Fig. 8). Thaler and also Tanasevitch had already used the appropriate term 'superspecies'. That the subunits had already achieved full biospecies level was confirmed in at least one case: a locality is known where the otherwise allopatric species *L. mansuetus* and *L. aridus* (Thorell, 1875) were found to occur sympatrically; there was not even a single intermediate individual (see Fig. 6, arrow).

Why superspecies with allospecies as subunits?

Pure application of the superspecies concept is primarily a matter of correct terminology and should not be misunderstood as an *explanation* of the biological background. But genital structures and what was formerly called the 'lock-and-key principle' (Dufour 1844) may provide the key for a biological interpretation of the origin of allospecies patterns. Two aspects should be considered: a) It is generally supposed that complex genital structures in terrestrial arthropods are extremely sensitive in reflecting genetic differences (see e.g. Arnqvist 1997), and b) the need for an optimal co-adaptation between male and female copulatory organs. Both factors are interlinked. As already explained, there are many

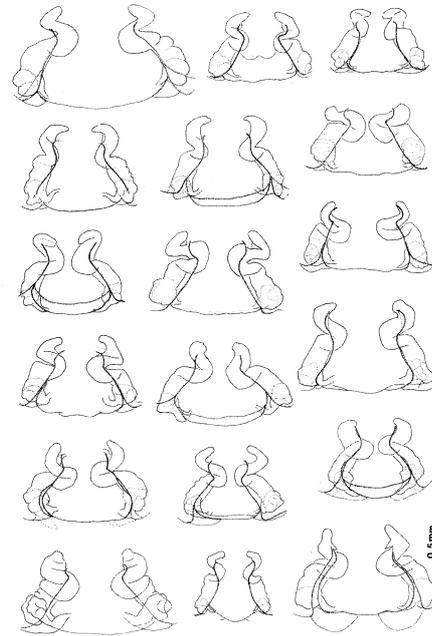


Fig. 9. Intraspecific variation of vulvae of *Stegodyphus dufouri* specimens from different localities in northern Africa, Aden, the Sudan, Mali and Niger (from Kraus & Kraus 1988).

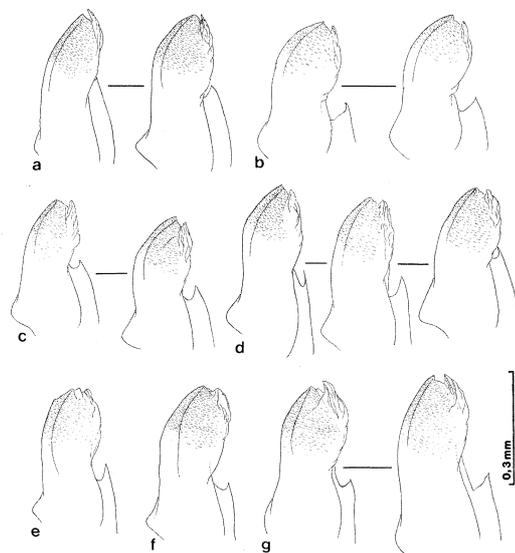
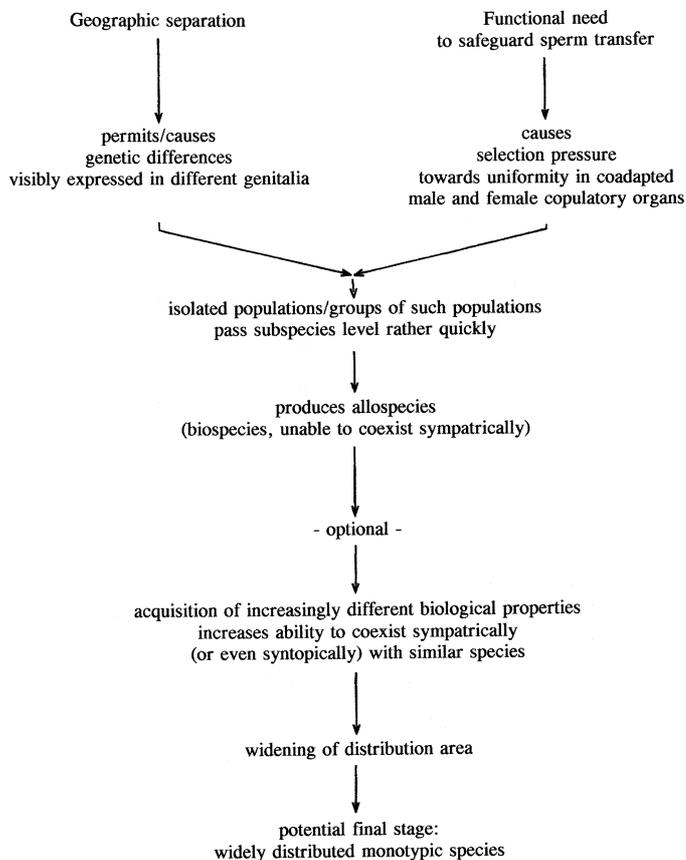


Fig. 10. Intraspecific variation of terminal lamellae of male bulbi of *Stegodyphus mimosarum* specimens from the Congo (a), the Serengeti (b), Durban (c), Natal (d), the Kruger Park (e), the Transkei coast (f), and Madagascar (g) (from Kraus & Kraus 1988).

Fig. 11. Hypothesis: Diagram illustrating the possible origin of allospecies, including the potential ability to coexist with similar species at later stages of evolutionary divergence.



examples of comparatively slight but regionally invariable genital differences. This is not only true for species complexes in spiders, but has also been found in the Lepidoptera and in many other arthropod groups, carabid beetles included (for review, see de Lattin 1967). Optimal coadaptation has been extensively discussed by Eberhard (1985). He believes in selection by female choice (see Arnqvist 1997). However, in spiders female choice may be highly dangerous for males and could probably cause unbalanced sex ratios. Hence, any selective advantage of female choice seems to be doubtful; it was apparently not found to occur in nature. Furthermore, male bulbs are not innervated at all, and corresponding (tactile) receptors remain to be discovered in sclerotized female copulatory organs.

Instead, the function of complicated cou-

pling mechanisms simply seems to safeguard sperm transfer (Kraus 1968), in some instances by more than one copulating male (see Wiehle 1967). It is this requirement that apparently stabilizes details of copulatory organs. Loerbroks (1983) demonstrated that limited variability may be observed in the epigynes but not in the vulvae of certain thomisid spiders. Similar variation was observed by Kraus & Kraus (1988) in female specimens of African Eresidae, especially in *Stegodyphus dufouri* (Audouin, 1826) (Fig. 9), and in the male terminal lamella (Fig. 10) of *S. mimosarum* Pavesi, 1883. This kind of slight variability remains within narrow limits and does not seem to influence perfect function.

The hypothesis deduced is as follows: The main function of coupling mechanisms is to safeguard sperm transfer. Almost perfect homogeneity of the functioning components of both

male and female genitalia is of high selective advantage. Less perfect mutual adaptation is regarded as counterproductive. Selection pressure favors uniformity and obliterates deviations. Two mechanisms may shorten transitory phases at a subspecies level and hence accelerate the formation of distinct allospecies:

—the expression of genetic differences in genital structures in geographically separated populations (or in separated groups of intercommunicating populations, respectively), and
 —selection pressure towards optimal coadaptation of male and female copulatory organs within such units, i.e. the origin of obligatory allopatric biospecies (Fig. 11).

All progressive transitions — from allospecies to regular species — can be expected when the efficiency of primarily unsolved problems of coexistence becomes increasingly reduced by the acquisition of diverging biological properties.

An alternative hypothesis would be most welcome, but I am presently not aware of another conceivable model. One possible way of testing the hypothesis presented here would be to investigate whether there could be any correlation between the occurrence of allospecies in spiders and the presence of coadapted complex, instead of comparatively simple, genital structures.

PERSPECTIVES AND FUTURE QUESTIONS

1. Zones of contact between allospecies should be studied.
2. As chromosomal differences between allospecies have been observed in many other animal taxa, future studies should include appropriate analyses; in spiders, the present information is close to zero (for details see e.g. White 1978).
3. The problem of tens of thousands of independently described species without subspecies can be solved by applying the superspecies concept. Instead of just 'stamping' the morphospecies, this approach would lead to a better integrative understanding of evolutionary and especially of biogeographic interdependencies.

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