

The significance of copulatory structures in spider systematics

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Introduction

Before the 'Golden Age of Araneology' (1850-1900: Bonnet 1945), copulatory organs played a minor role in descriptions of new spider species and in the establishment of relationships. Most emphasis was on descriptions of 'somatic' characters like body shape, eye positions, leg spination, color patterns, etc. Copulatory organs were mentioned as accessory characters at best.

Very soon, however, a realization took hold that had been established earlier in entomology (e.g. Dufour 1844): that superficially similar species are often easily distinguished by their genitalia. And this is true in spiders even though the anatomical basis is very different from that in insects: while insects copulate with appendages (gonopods) of their posterior abdominal segments, spider males transfer sperm with unique structures on their pedipalps into the female copulatory opening(s) on the second opisthosomal segment. The spider taxonomist who faces a species that is not easily identified by its general appearance will generally study just the male palp and the female external genitalia (the epigynum) and will often not need a further look at eyes, spinnerets, legs, etc. to determine the species. Modern alpha-taxonomic works on spiders typically contain detailed descriptions and illustrations of copulatory organs, while all other structures have shifted to the background in comparison. This is most conspicuous in species-rich genera where up to dozens of very similar species are distinguished primarily by their copulatory organs (e.g. Gertsch 1982, Bosselaers & Jocqué 2000, Platnick 2000, Huber 2001). Cases of considerable variation of copulatory organs (e.g. Lucas & Bücherl 1965, Levi 1968, 1974, Sierwald 1983, Kraus & Kraus 1988, Pérez-Miles 1989, Huber 2000; see also Goulson 1993, Hribar 1994, Johnson 1995, Tanabe & Shinohara 1996) have been and still are (rightly or not) considered exceptions.

Copulatory organs in this context are not just those organs that transfer and accept sperm ('primary copulatory organs'). A variety of other structures ('secondary copulatory organs') in different spider families come into action during copulation, e.g. processes on the male legs that hold the female (Coyle 1988), modifications of the male chelicerae that are used by the male to position himself correctly in relation to the female (Huber & Eberhard 1997), or protuberances on the male head that are grasped by the female (Schäible et al. 1986). All these structures are useful in distinguishing closely related species, meaning that they often evolve faster than other morphological characters and that they tend to show discontinuous interspecific variation. The same seems to hold true for spider behavior that is associated with pairing, like optical or vibratory courtship signals (Grasshoff 1964, Hollander & Dijkstra 1974, Barth 1990, Knoflach 1998, Uetz & Roberts 2002). New studies support the idea that relatively rapid evolution of characters associated with mating is not restricted to morphology and behavior but may be common at the level of molecules, too (Eberhard & Cordero 1995, Rice 1998, Palumbi 1998, Gavrillets 2000, Swanson & Vacquier 2002). To which degree these characters can be used in a molecular taxonomy (cf. Westheide & Hass-Cordes 2001) and are congruent with

morphological (and behavioral) characters, is a field that is only just developing (Tautz et al. 2003, Seberg et al. 2003, Lipscomb et al. 2003).

A similar trend towards an increased emphasis on copulatory organs can also be observed in phylogenetic research. Traditionally, genera and higher taxa in spiders are defined rather by non-genital characters (Platnick 1975: "As is usual in spiders, the genera are defined by somatic characters and the species groups by genitalic characters"; see also Griswold 1993, Foelix 1996). Even though in modern phylogenetic research *a priori* weighting of any class of characters is widely considered subjective and therefore unscientific (Kitching et al. 1998), copulatory organs have increasingly taken a strong or dominant position by the following detour: the often high complexity of these organs provides a wealth of separate characters which, in sum, account for a considerable part of the data matrix (38% of characters in Scharff & Coddington 1997, 46% in Bosselaers & Jocqué 2000, 48% in Huber 2003, 76% and 62% respectively in Hormiga 1994, 2000, 63% and 53% respectively in Griswold 1990, 1993, 77% in Wang 2002; all these values are approximations as the assignment of characters to copulatory organs is sometimes not unambiguous). In sum, while some qualitative features often account for the significance of copulatory organs in alpha-taxonomy, it is rather a quantitative feature, i.e. the large number of informative characters, that account for their importance in phylogenetic research.

Two questions follow from the postulate that the morphology of copulatory organs delimits species: what are species, and why (if at all) is it the copulatory organs that delimit species most clearly in spiders (and many other groups of animals)?

The species concept(s) of spider systematists

What a species is (ontology) and how we may recognize it as such (epistemology) has troubled systematists for many decades and still provides ample substance for hot debates and resentments (Wheeler & Meier 2000). This is all the more remarkable as, according to Wilson (1992: 38), species are "intuitively obvious entities" and the species concept is something like "the grail of systematic biology". Ehrlich's (1961) prophecy that electronic data processing would result in an upheaval in zoological systematics has largely come true in phylogenetic research, but definitely not with regard to a solution for the species problem.

Almost anything is up for discussion: Do we need a universal species concept or do we accept a pluralism of concepts? Is it primarily about what species are or about how to recognize them [Herre's (1964) "Artsein" vs. "Artkennzeichen"]? Are species epistemologically the basis for phylogenetic analysis or the result of it? Does it need a "feeling" (Mayr 2000) to recognize species or are there any objective criteria? This list could be continued *ad libitum*, and the diversity of opinions and convictions is clearly reflected by Mayden's (1997) list of no less than 22 contemporary species concepts.

Considering this immense number of concepts, it is surprising that in spider taxonomic papers the underlying species concept is usually not mentioned at all. Few arachnologists have taken a more or less clear stand in this regard, either in the context of revisions or in separate publications (e.g. Grasshoff 1968, Martens 1969, Levi 1973, Kraus 2000, Wheeler & Platnick 2000). In part, this apparent neglect may be due to simple ignorance of the problem, and in part also to the impression that this is a purely academic and therefore an empirically irrelevant issue. On the other hand,

there seems to exist a tacit agreement that might be characterized as follows: 1. Species are not purely human constructs but do exist in reality, marking a natural boundary between tokogenetic and phylogenetic relationships. 2. Species are reproductive communities that are genetically isolated from other such communities, i.e. there is no considerable exchange of genetic information and evolution may proceed relatively independently in different species; this also implies that the species concept is not universal. 3. In principle, all characters showing discontinuous variation are considered as potential indicators of species limits, but copulatory organs often take the decisive role: individuals with identical copulatory organs but with discontinuities in other characters are usually interpreted as morphs of a polymorphic species (when in sympatry) or as subspecies of a polytypic species (when in allopatry).

While the first two points are about the ontology of species and have little impact on the practical work of spider systematists, it is the third point that usually decides what is treated as a species, what as a morph, a subspecies, or simply a variety.

In sum, even though the species concept of spider systematists cannot be simply dismissed as purely morphological or even as typological (in Cuvier's sense), it is true that the epistemological aspect plays a decisive role. Demands, like those by Bonik et al. (1978), for a recurring justification of why certain characters rather than others are considered to indicate species limits have barely provoked any perceptible echo. The potential logical circle that the current theory and practice entail (postulate: species are different in their copulatory organs ↔ practice: individuals with different copulatory organs are described as different species) will be taken up again below.

Why are copulatory organs species-specific?

The multitude of species concepts faces a similar multitude of hypotheses that have been put forward to explain species-specificity of copulatory organs (Eberhard 1985, Edwards 1993, Arnqvist 1997). Largely refuted is Dufour's (1844) lock-and-key hypothesis according to which differences in genitalia are interpreted as isolating mechanisms ("la sauvegarde de la légitimité de l'espèce"). A wealth of evidence as well as theoretical considerations have been brought forward against it (e.g., missing morphological basis: Gering 1953; no character displacement in sympatry: Ware & Opell 1989; hybridization in spite of different genital morphology: Porter & Shapiro 1990; see also Kraus 1968, Eberhard 1985, Shapiro & Porter 1989, Arnqvist et al. 1997; but see Blanke 1980, Berube & Myers 1983, Mikkola 1992, Sota & Kubota 1998). Still unclear is the significance of Mayr's (1963) pleiotropism-hypothesis according to which genetic links between copulatory and other structures result in an accumulation of selectively largely neutral changes in the former (see Eberhard 1985 vs. Jocqué 1998, Arnqvist et al. 1997). The idea of genital extravagances partly representing selectively neutral luxuries is propagated at regular intervals (e.g. Müller 1957, Kraus 1968, Goulson 1993), but these claims are based on negative data only (no obvious function found) and are also doubted for theoretical reasons (Eberhard 1985). Kraus (1984) proposed a correlation between complexity of genitalia and circumstances of copulation (e.g. aerial vs. on firm ground in insects; on mating thread or web vs. on firm ground in spiders). However, species-specificity is independent of complexity, requiring an additional (or different) explanation.

A watershed in the style of argumentation was Eberhard's (1985) 'Sexual Selection and Animal Genitalia'. The author discusses previous hypotheses and contrasts them with Darwin's (1871) female choice hypothesis applied to copulatory

organs. According to this, genitalia are not just sperm-transfer organs but at the same time courtship organs ('competitive signalling devices': West-Eberhard 1984) that evolve because they initiate processes within the female that make it more probable that the male's own sperm will be used instead of that from competitors. Critical aspects in this case are the continuous competitive pressure among conspecific males, the wide scope and unpredictability of female preferences, and the impossibility for the male to ever reach an 'optimal' solution (West Eberhard 1983, 1984).

Eberhard's (1985) book has re-ignited the controversy, it has stimulated research that supported his view (e.g. Rodriguez 1995, Arnqvist 1998, Arnqvist & Danielsson 1999, Tadler et al. 1999, House & Simmons 2003), and it has induced new hypotheses, partly as modifications, partly in diametrical opposition. Whether or not the mostly still limited distribution and acceptance of these new ideas is due to their recent publication, the future will show.

Alexander et al. (1997) formulated the 'conflict of interest' hypothesis, according to which males and females are involved in a constant arms race, trying to gain or retain control over mating and the fate of sperm (see also Arnqvist & Rowe 2002). The crucial difference with the female choice hypothesis is not the conflict of interest per se (which is beyond question) but the issue about whether females cooperate selectively (in terms of genital morphology in this case) or resist indiscriminately. Or, in other words, whether females, parallel to the evolution of the male traits, evolve a preference for or a resistance against them (Holland & Rice 1998). One prediction of the 'conflict of interest' hypothesis is that in groups where females have the behavioral control over copulation and males are forced to court and lure them before copulation, the copulatory organs should be rather uniform and simple. Spiders clearly contradict this prediction (Huber 1998).

Jocqué's (1998, 2002) 'mate check' hypothesis picks up both Mayr's (1963) idea of genetic links between copulatory and other characters and Dufour's (1844) idea of male legitimization. Species-specific copulatory organs are considered 'guarantors' for the presence of some essential adaptation(s) (not necessarily morphological). If the adaptation is not 'exteriorized', i.e. made perceptible for the female, it will most likely disappear again. Female choice in the conventional sense is here seen as a consequence rather than a cause of species-specific copulatory organs.

Notwithstanding all the differences in starting points and explanations, one substantial similarity may be emphasized: the three more recent hypotheses all view copulatory organs beyond their primary function also as signaling devices, as communicatory structures. Against the background of this emerging consensus, the question about the content of the signals involved and about the universality of individual hypotheses appears secondary, if not less exciting.

Biases, constraints and logical circles

If species are considered genetically isolated reproductive communities, and if copulatory organs are not involved in reproductive isolation, then there is no compelling reason to expect a tight correlation between reproductive communities and groups of individuals delimited by reproductive morphology. In this sense, the idea mentioned above about potential logical circles is taken up here again, together with some related problems resulting from common taxonomic practice.

Considering the fact that the taxonomic literature has been playing a vital role in the formulation of hypotheses on the evolution of copulatory organs [e.g. in

Eberhard's (1985) comparative morphological approach], the following question arises: is there any evidence for biases, constraints, or logical circles in taxonomic practice that might be partly responsible for the apparent phenomenon of species-specificity and relatively rapid evolution of copulatory organs? Three points will be discussed here: the impact of the hypothesis 'genitalia are species-specific' on the discovery of genital polymorphisms and polytypisms, and the problem with small sample sizes. A more detailed account of this and related topics has been published recently (Huber 2002).

1. *Polytypisms*. It is usually easy to distinguish different species from a limited geographic area (and a limited time horizon). In such a situation, sometimes called 'nondimensional' by biologists (Mayr 1955), copulatory organs have proved to be excellent diagnostic characters at species level. The common impression that genitalia vary less within species than other structures was largely supported by a large morphometric analysis of several insect and spider species (Eberhard et al. 1998; see also Arnold 1986, Teder 1998, Palestini et al. 2000, Tatsuta et al. 2001). However, in order to admit comparisons among species, each species in that study was represented by individuals of one local population. But the term 'species-specific' is about species, and species have a spatial (and temporal) distribution. Characters that are taxonomically useful in the nondimensional situation may become ambiguous as soon as geographic variation and hybrid zones are included in a study (e.g. Leong & Hafernik 1992, Tanabe et al. 2001).

Traditional taxonomic works had and often still have a regional emphasis, and even modern, taxon-oriented works sometimes seem based on a species concept that worked fine in this nondimensional situation (i.e., a typological species concept). Starting from the observation that copulatory organs are species-specific at one place, we extrapolate to allopatric populations and, given the case that differences in the copulatory organs are found, assign these to different species. This step constitutes not just a venture (like any extrapolation: Herre 1964), but it justifies our original assumption about species-specificity, closing a logical circle.

Two further observations are relevant in this context: (1) Exactly in those groups of animals in which Mayr's (1963) concept of polytypic species has found wide support (birds, mammals, butterflies, snails; Mayr & Ashlock 1991) genitalia are (or were originally) not used for species identification. (2) A high percentage of known invertebrate species are known from the type locality only (e.g. 45% and 53%, respectively, in samples of beetle taxonomic papers cited in Stork 1993, 1997).

2. *Polymorphisms*. In contrast to the previous point, this is about species that show discontinuous variation within populations. While this phenomenon is quite common in many groups of animals, there are very few cases documented about genital polymorphisms (Müller 1957, Kunze, 1959, Inger & Marx 1962, Ulrich 1988, Johnson 1995, Mound et al. 1998, Hausmann 1999, Huber & Pérez, 2001a). The crucial question here is: how often does it happen that different morphs of one species are described as different species? This issue was discussed in detail recently (Huber & Pérez 2001b) with the conclusion that with the data available at this point it is not possible to decide objectively whether the cases cited above are rare curiosities or rare discoveries of a widespread phenomenon. Recent findings that genitalic morphology can be significantly affected by conditions during ontogeny (e.g. Hribar 1996, Arnqvist & Thornhill 1998) suggest that at least seasonal polymorphisms (actually polyphenisms) like those in some insects (Müller 1957, Kunze 1959, Vitalievna 1995)

may be quite common. Jocqué's (1998) 'mate check' hypothesis even predicts that genital polymorphism should be a common phenomenon in the course of sympatric speciation (Jocqué 2002).

Beyond such speculations we can state with some confidence that methodological and practical aspects of taxonomic work act together in a way that makes the discovery of genital polymorphisms very unlikely in the first place: (a) the basic assumption of species-specificity and the dominance of genitalia and other sexually selected characters in species delimitation (Eberhard 1985: 153, Zeh & Zeh 1992, Huber 2002, Jocqué 2002); (b) the absence of data on the biology of the vast majority of invertebrate nominal species (Stork 1997); (c) the constraint of small sample sizes. The last point is treated separately as it has implications not only for our ability to discover polymorphisms but for the assessment of variation in general.

3. *Sample sizes.* If the majority of species is known from a few specimens from a single locality, what general statement can we make about variation, morphoclines, overlapping or non-overlapping frequency distributions; in short, about species-specificity? Modern biology focuses, with some justification, on a relatively minute proportion of the world's biodiversity (human, rat, fruit-fly, etc.). To some extent, this obscures the fact that about the vast majority of 'known' species we know literally nothing.

A quantification of this statement is difficult, but was attempted recently with two data sets (Huber 2002): The first included all 787 species of the spider family Pholcidae known as of January 2002. The second was a sample of nine recent spider taxonomic monographs on various different families (including 938 species descriptions). The result was not necessarily surprising (for similar data on beetles, see Erwin 1997), but disillusioning nevertheless: 40% and 53% of species, respectively, were known from less than four specimens; 24% and 31%, respectively, were represented by singletons. In 33% and 49%, respectively, only one sex was known.

It is obvious then, that in a discussion on species-specificity, we must exclude a high percentage of known species. The only option we have is to extrapolate from the rest, whatever its size. In the case of pholcid spiders, it turned out that only 29 species were sufficiently well known to decide on the question of genital polymorphism as an example. Given the fact that genital polymorphism is known in one pholcid species, it is more correct to take as a basis the ratio of 1/29 rather than 1/787. Therefore, the (admittedly vague) prediction is not that genital polymorphisms are common, but 20 times more common than previously assumed anyhow.

Even more problematic is a quantification of 'sufficiently well known' species in well studied areas, like Europe (Huber 2002). The fact, however, that genital polymorphisms were discovered by chance in all cases underlines our ignorance about the real frequency of this phenomenon and the necessity of projects specifically designed to address such problems.

Conclusion

Even though copulatory organs play a decisive role in spider systematics, especially in alpha-taxonomy, there is ultimately no proof that they reliably indicate 'biological' species limits: (1) the lock-and-key hypothesis, developed within a typological context, is considered largely refuted; (2) numerous studies document considerable intraspecific variation in spider copulatory structures; (3) sibling species with

indistinguishable copulatory organs are being discovered at an increasing rate. Relatively rapid evolution of copulatory structures is very probably a fact, but this characteristic may equally apply to characters that are more difficult to study (like pheromones, courtship patterns, etc.) but that function as isolating mechanisms and are therefore possibly much more reliable indicators of species limits. A renewed emphasis on research on variation, as well as congruence analyses between morphological and molecular data are most likely to advance our understanding about the significance of copulatory structures in systematics.

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