The Importance of Biosemiotics for Morphology

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Abstract

Morphology and its relevance for systematics is a promising field for the application of biosemiotic principles in scientific practice. Genital coupling in spiders involves very complex interactions between the male and female genital structures. As exemplified by two spider species, *Nephila clavipes* and *Nephila pilipes ssp. fenestrata*, from a biosemiotic point of view the microstructures of the male bulb's embolus and the corresponding female epigynal and vulval parts form the morphological zone of an intraspecific communication and sign-interpreting process that is one of the prerequisites for sperm transfer. Hence these morphological elements are of high taxonomic value, as they play an essential role in mating and fertilization and consequently in establishing and preserving a reproductive community. Morphology clearly benefits from a biosemiotic approach, as biosemiotics helps to sort out species-specific morphological characters and to avoid problematic typological interpretations.

Keywords Biosemiotics · Character interpretation · Morphological characters · *Nephila clavipes* · *Nephila pilipes ssp. fenestrata* · Recognition window · Reductionism · Species problem

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Introduction

In his preface to Barbieri's (2003) work, "The organic codes", the evolutionary biologist Ghiselin (2003: ix) pointed out:

"Most scientific publications deal with problems that can be explained in a straightforward manner and with solutions that can be evaluated as a matter of routine. But scientific progress often occurs when somebody tries to *reformulate* the problem, or to suggest a different kind of solution. When that happens, it may be necessary to dwell as much upon the questions as upon the answers, and to show how a *novel approach might give further significant results.*" (italics ours)

Taking this citation as an inspiration, the purpose of our paper is to show by an example from spider taxonomy that biosemiotics as a novel approach has the potential to overcome widespread and straightforward, but insufficient explanations concerning the function of specific morphological structures in spider genital organs. In this way biosemiotics simultaneously contributes to restrengthening morphology, which has experienced a severe decline starting in the twentieth century.

Biosemiotics, which studies the production and interpretation of signs and codes in living systems (Favareau 2010; Kull 2016), is essentially derived from Peircean semiotics, but also from more zoologically oriented roots such as Jakob von Uexküll's concept of Umwelt (Kull 1999), then general system theory, later cybernetics, information theory etc. Based on these origins biosemiotics is an interdisciplinary attempt to capture the diversity and complexity of living systems. The central notion of biosemiotics is "sign". A sign represents an object and is interpreted by a sign receiver. The object can be abstract, i.e. without physical referents, or concrete. Drawing on Peircean semiotics Laubichler (1999) states that whatever biology works on, be it measurement data, molecular or morphological structures, it is representamina or sign vehicles, not objects. Taking into consideration the manifold interactions of life as signs biosemiotics is able to integrate a series of biological phenomena that previously were unrelated and not compatible with each other. The basic idea is that biology is based on communication processes on all levels, from the molecular level to ecosystems (Gérard 2014), so that life processes can be viewed as sign-mediated interactions. Life phenomena are, in all aspects, natural semiotic systems. Permeating the entire biology, the sign is a useful key and a practically relevant access to the understanding of life. The connection between biology and semiotics is characterized by Pattee (1995) as follows: "Communication is the essence of life." A particularly lucid and catchy explanation of what biosemiotics is about has been given by Kull (2016: 61):

"A semiotic approach in biology means the study of the organisms' own approach, the study of distinctions that they make, what they recognise, what they intend, what they know, in a broad sense."

At present, however, there is only a slowly spreading tendency of incorporating biosemiotic principles and approaches in the biosciences (Hoffmeyer 1997: 2;

Laubichler 1999: 420; Barbieri 2003, 2008; Favareau 2010: 62–63; Gálik 2013: 860), such as ecology (Maran 2017), ethology (Delahaye 2019), molecular biology (Jerne 1985; Nossal 1987; Sercarz et al. 1988; Eder & Rembold 1992; Faria 2008) and neurophysiology (Freeman 1998; Olds 2000; Cariani 2001; Freeman & Rogers 2002). A comparison with earlier assessments of biosemiotics' actual role in the life sciences (Todt 1987: 425; Hoffmeyer 1997: 2; Kull 1999; Laubichler 1999: 420; Kull 2004; Schult 2004: 101) shows that the situation has hardly changed since the 1980s and 1990s. The acceptance of biosemiotic principles, albeit relatively limited, may be explained by the extreme amounts of biological data, the dynamics and the enormous number of interactions among living things and with their environment that make the limitations of the reductionist approach clear, and therefore necessitate the search for new approaches (Deppert 1992; Eder & Rembold 1992).

A broader acceptance of biosemiotic principles in the biosciences can only be expected if it is clearly demonstrated how biosemiotics is able to offer new insights that are out of the reach or scope of other, more established disciplines and go beyond a mere description or reformulation of known facts in other, semiotic terms. In our paper we want to show that a biosemiotic approach is able to identify species-specific morphological characters in spiders that have gone unnoticed so far.

Biosemiotics and Zoological Systematics: Overcoming Typology, Restrengthening Morphology

Over the course of the twentieth century morphology has suffered a dramatic loss of significance within the biological sciences (Riedl 2006). In particular, morphological taxonomy is regarded by many as a dying discipline (Bik 2017). Already around 1900 the discovery of morphologically indistinguishable but reproductively isolated sibling or cryptic species on the one hand and on the other hand of highly distinct intrapopulational variants in one and the same species revealed that a merely morphological species concept was insufficient (Mayr 1992; 2000). Generally speaking, the dominant position previously held by the morphological species concept was taken over by the biological species concept, defining species as groups of interbreeding natural populations that are reproductively isolated from other such groups (Mayr 1940: 256, 1942: 256). However, we should bear in mind that there are more than 20 different species concepts (Mayden 1997; Lloyd 2001). In his defense of the biological species concept Mayr argued that the morphological species concept was typological. Mayr's equation of morphological and typological species, although heavily criticized by others (Wheeler and Platnick 2000; Knapp 2008), still reflects a common attitude. Also, Hennig, the founder of the influential phylogenetic species concept, argued against an uncritical use of similarity relationships and rejected a purely morphological definition of species, which he considered typological (Hennig 1966: 43–44, 78–80, 148, 239; Wiley and Mayden 2000).

Even if a purely morphological species concept is worthy of criticism, one must not forget that a recurrence to morphological characters can be helpful to identify reproductive communities. Within the biological species concept based on reproductive isolation, those morphological traits that are involved in pre-mating isolating mechanisms such as behavioral isolation and mechanical isolation have gained considerable

weight (Mayr 1970: 57). Another species concept based on sexual reproduction is Paterson's recognition concept of species, where the members of a species share a common fertilization system, a subset of which is the Specific-Mate Recognition System (Paterson 1985, 1988; Masters et al. 1987; Lambert and Spencer 1995; Stamos 2003: 197–199; Mallet 2013: 682–683). Among the characters contributing to the recognition of an appropriate mating partner and the achievement of fertilization Paterson (1988: 69) mentions “coadapted signals and receivers of mating partners, and their coadapted organs of gamete delivery and reception”. This reference to the signal function of characters, often morphological ones, shares a common perspective with biosemiotics (Favareau 2010; Kull 2016). Accordingly, Kull (2016) states that Paterson's “recognition concept of species is basically communicational and semiotic” and that the “biosemiotic conception of species largely stems from the work of Hugh Paterson”, while its origins can be traced back as far as Peterson's (1903, 1905a, b) works on the origin of species by physiological isolation. Central to the biosemiotic species concept is the notion of an individual's recognition window. In biparental reproduction, the recognition window is responsible for dividing potential partners into compatible and incompatible ones. Thus, it is a decisive factor for producing species and holding them together.

To sum up, focusing on and identifying those morphological structures that are crucial for the recognition of potential reproductive partners, or essential for successful copulation, sperm transfer and fertilization, are a suitable means to free morphology from recurrent and well-trodden reproaches of being “typological”. With our paper we would like to join the ranks of those who have already stressed the importance of biosemiotics for morphology in other contexts, such as mimicry and visual communication (Kleisner 2008a, b, 2015; Kleisner and Maran 2014; Brejcha and Kleisner 2016; Maran 2017; Kleisner and Saribay 2019).

The Application of Semiotic Principles in Spider Taxonomy

Some General Remarks on Spider Taxonomy

For practical reasons taxonomy in spiders mainly uses morphological characters. Its interest focuses on the genitalia, that is the male secondary copulatory organ (palpal bulb) and the female reproductive organs, as determining taxonomical relationships and phylogeny requires more than a superficial comparison of similarities between indiscriminately chosen traits. However, as we will see, it is often the case that when it comes to analyzing the structure of the spiders' reproductive organs authors are content with depicting and describing every detail without singling out those parts that are decisive for intraspecific communication processes. Thus, one might argue that while choosing the reproductive organs as basis for the establishment of spider taxonomy is clearly not typological, the way in which the reproductive organs are described is often “extremely typological” (Eberhard and Huber 2010: 255). In our view it is a dangerous oversimplification to state that, because “the bulb of a male spider fits only into the genital opening of a female of the same species, [...] the shape of all bulb components is species specific” (Quade et al. 2019).

Male spiders do not have primary copulatory organs. Instead, the distal end of the last segment of the palpus (the second pair of appendages), the tarsus (cymbium), has been modified to transfer sperm. This genital appendage of the male's palpus, the so-called bulb, is more or less complicated in structure. The corresponding female copulation organ (vulva, epigyne) is also very diverse among different species. During copulation, the palpal organ of the male is partially inserted into the female's genital opening, which lies hidden in the epigyne's epigastric furrow and leads into the fertilization duct. The mutual morphological fit between the male and female structures is a prerequisite for successful sperm transfer (see also Foelix 2011: 226 sqq., Comstock 1910: 161 sqq.). The external sexual organs are often so specific among different species that they are used by systematists as an important feature in differentiating species. However, usually it is not taken into account that only very specific areas of the male's bulb are complementary to certain parts of the female's genital structure and have a communication function.

Publications referring to genital structures in spiders – to mention only a few, randomly selected studies (Engelhardt 1910; Gerhardt 1921; Gering 1953; Levy 1991; Uhl 2000; Burger & Kropf 2007; Jäger & Wunderlich 2012; Zakharov & Ovtcharenko 2013; Jäger 2015) – usually contain highly detailed drawings of these structures. Yet only a few authors describe the interrelation between the genital structures of the two sexes at all. Sierwald (1984: 411) shows an embolus that got stuck in the vulva. Grasshoff (1968, 1973) gives a very detailed account of the genital-morphological structures and their function in spiders of the subfamily *Araneinae*, based on his investigation of animals preserved in copula. Loerbroks (1984) examined structure and function of the male and female genitalia, including coupling mechanisms in *Misumena vatia*, Schult (1983) and Schult and Sellenschlo (1983) in *N. clavipes* and *N. pilipes ssp. fenestrata*. Loerbroks (1984: 397) even proposed a technical model of the coupling mechanism. Though very precise and complex, these investigations do not express the communicative and biosemiotic aspect, that is, they do not focus on the complementary areas of the bulb and the female genitalia. This is due to a quasi-typological approach, whereas the application of biosemiotics involves different research methods and perspectives. That shows how theory impacts research findings.

Huber (1993) was the first to combine the method of freeze-fixation of spiders in copula and subsequent preparation of serial sections of the copulatory organs in functional contact. His numerous publications on genital mechanics and copulatory mechanisms mainly in Pholcids contain highly detailed morphological studies of the genital structures and their function (Huber 1994a, b, 1995a, b, 1997, 1998, 1999, 2002; Huber & Eberhard 1997). Huber (1993) also raises the important question of whether the female can evaluate the mechanical fit of those structures of the male copulatory organ that come into contact. He concludes (Huber 1993: 2445) that “although receptors could not be found in the female's contact zones, tactile stimulation cannot be definitely excluded. There might be undiscovered internal receptors in the membranous parts of the epigastric furrow and the genital pouches.” With his concept of “contact zones” and his idea that the genital structures’ coming into contact might be perceived by the female (and thus function as a sign for the female, one might add) Huber's approach has a lot in common with a biosemiotic point of view. Furthermore, he (Huber 2002: 105) remarks that the „taxonomic literature provides a wealth of illustrations, mainly of the genitalia” and that these “simple drawings are usually

sufficient for species identification, but rarely provide any detail.” And it is precisely these details that can be decisive for species recognition. Elsewhere, Eberhardt and Huber (Eberhardt & Huber 2010: 255) use the term “cooperative structures”, which connotes communication processes. Huber’s studies certainly contain biosemiotic principles, without explicitly mentioning this term.

The Spider Species *Nephila clavipes* and *Nephila pilipes* ssp. *fenestrata* as Case Studies

Several studies of the functional morphology of spider genitalia have shown that genital coupling in spiders involves very complex interactions between the male and female genital structures (Grasshoff 1968, 1973; Huber 1993, 1994a, b, 1998; Uhl et al. 1995, 2007). From a biosemiotic point of view not only mate recognition constitutes a communication process, but also the fitting between coadapted male and female genital structures can be regarded as a sign whose interpretation leads to certain effects, such as sperm transfer. Using two species of the spider genus *Nephila* as an example, in what follows we will show that a biosemiotic approach opens new perspectives on how to assess the taxonomic value of morphological characters.

As early as 1960 Hermann Wiehle provided a fundamental, but unfortunately little-noticed contribution about the embolus of the male bulb and functional correlates between structures of the bulb and of the epigyne resp. vulva (Wiehle 1960) in a large number of spider species. Certainly, his emphasis that all considerations about the form of the embolus take into account the construction of the corresponding vulva in order to enable explanations through this correlation (Wiehle 1960: 480) was a step in the right direction. Nevertheless, Wiehle’s illustration (1967: 195, Fig. 47) of the bulb and embolus of “*N. madagascariensis*” omits essential species-relevant features. Moreover, his depiction of the pedipalp seems to have been falsely assigned to *N. madagascariensis*. Although the drawing is very imprecise, a comparison with drawings of the bulb of *N. clavipes* (Pickard-Cambridge 1901: Pl. VII; Levi 1980: 19, 21; Heimer 1982: 46; Schult & Sellenschlo 1983: 223; Levi & Eickstedt 1989: 51; Hormiga et al. 1995: 332) and of the bulb of *N. madagascariensis* (Saaristo 1978: 120; Saaristo 2010: 95) by other authors suggests that this is not the bulb of *N. madagascariensis*, but of *N. clavipes*. Wiehle’s error may be due to the fact that the tip of the embolus was not the focus of his investigations. Unfortunately, the remaining literature on *Nephila* species (Karsch 1879: 838; Gerhardt 1933; Archer 1958; Heimer 1982; Schult 1983; Liao et al. 1984: 68; Clausen 1987; Barrion et al. 1988; Higgins 1989: 749; Reiche 1992: 12; Uhl & Vollrath 1998: 45; Schneider et al. 2001; Ramos et al. 2005: 1993; Fromhage & Schneider 2006; Kim 2006: 208; Harvey et al. 2007: 422; Kuntner & Coddington 2009; Kuntner et al. 2009a, 2009b) also fails to provide sufficiently detailed information on the shape and function of the embolus.

Figure 1a (*N. clavipes*) from Schult and Sellenschlo (1983) does not show in sufficient detail the apical area of the bulb (encircled), that is the embolus, which is of interest here. The same applies to Fig. 1c from Wiehle (1967: 195, Fig. 47). In none of these figures is the function of the embolus clearly shown. Moreover, the corresponding female part was completely omitted. Figure 1d shows a hypothetical interaction of the complementary elements of the female’s epigyne and the male’s bulb. The tip of the bulb’s embolus (Et) is surrounded

Fig. 1 *Nephila clavipes*. **a** bulb, unexpanded state (left) and **b** expanded state (right), rectangle indicates tip of the bulb, *De* = ductus ejaculatorius, *E* = embolus, *Et* = embolus's tip, *bH/mH/dH* = basal, median, distal hematodocha, *C* = conductor, *Sp* = spermophor, *Sd* = distal part of the spermophor, **c** right pedipalp from lateral (falsely attributed to *Nephila madagascariensis* by Wiehle (1967)), “the embolus jumped out of its guidance” (Wiehle 1967: 195, translated); rectangle indicates tip of the bulb, **d** rectangle indicates morphological zone of an intraspecific communication and sign-interpreting process, conductor (*C*) lying in the epigastric furrow (*Ef*), embolus's tip (*Et*) inserted into the introductory opening (*Io*) of the vulva (schematic representation). **a**, **b**, **d** taken from Schult and Sellenschlo (1983), **c** taken from Wiehle (1967)

by the conductor (*C*) that lies in the epigastric furrow (*Ef*) of the female's epigyne. As the bulb's conductor is no closed tube, but laterally open, with increasing hemolymphic pressure it takes on the shape of a channel, so that the flagelliform tip of the embolus is no longer completely enveloped. Finally, the embolus's tip exits the conductor sideways and is inserted into the introductory opening (*Io*) of the vulva (Schult and Sellenschlo 1983). In *N. pilipes ssp. fenestrata* (Fig. 2) the situation is different from *N. clavipes* in that the conductor containing the embolus possesses a discrete terminal exit opening. Furthermore, the conductor's tip is bent, having the shape of a hook, and fits exactly into the pouch-like entrance area of the vulva's introductory duct (Fig. 2d) (Schult and Sellenschlo 1983)

From a biosemiotic point of view these mechanical descriptions are no sufficient analysis, as they do not take into consideration the communicational and

Fig. 2 *Nephila pilipes* ssp. *fenestrata*. **a** bulb, rectangle indicates tip of the bulb, **b** vulva (dorsal view), *Go* genital opening, *Id* introductory duct, *Rec* receptaculum seminis, **c** fitting of the bulb's tip into the pouch-like entrance area of the vulva's introductory duct (schematic representation), **a–c** taken from Schult and Sellenschlo (1983)

functional aspects of the whole process. It is reasonable to assume that the initiation of sperm transfer starts when the exit opening of the male embolus's ejaculatory duct has reached its optimal position by coming into contact with the opening of the female fertilization duct. The achievement of such an optimal position of the embolus can be considered a sign and sperm transfer its interpretation. We hypothesize that certain morphological details hitherto unnoticed in the embolus ensure that among the many possible ones only a specific position of the embolus causes sperm transfer. Only future scanning electron-microscopical and CT examinations can confirm or refute our hypothesis. But it should be mentioned that there are some indications from studies on other spider species that our assumption may be right. In *Argiope bruennichi*, judging by the shape of the sperm transferring part (e1 in Fig. 4D in Uhl et al. 2007) of the embolus, it seems that the correct position of the embolus and the exit opening of its ejaculatory duct is achieved when the embolus's sperm-transferring part lies completely against the inner wall of the atrium, an aspect that until now has not received the attention it deserves. Furthermore, first scanning electron microscope (SEM) photographs of the emboli of *Segestria florentina* and *Segestria bavarica* by two authors of this paper have revealed a conspicuous, hitherto undocumented spur-like structure at some distance from the embolus's opening (not yet published). Generally, detailed investigations of the morphological structure of the embolus are extremely rare.

Conclusion

As exemplified by two different *Nephila* species, from a biosemiotic point of view the microstructures of the male bulb's embolus and the corresponding female epigynal and vulval parts form the morphological zone of an intraspecific communication and sign-interpreting process that is one of the prerequisites for sperm transfer. Hence these morphological elements deserve peculiar attention. They are of high taxonomic value, as they play an essential role in mating and fertilization and consequently in establishing and preserving a reproductive community. As is well known, in addition to morphological structures there are a number of other factors, such as behaviour (Schneider & Andrade 2011), pheromones (Gaskett 2007), habitat, courtship periods etc., that either prevent mating between species or enhance specific mate recognition and the achievement of fertilization. Therefore, even with compatible morphological structures, a reproductive community cannot be assumed for sure. However, if a match fails between structures that are necessary for communication processes involved in the recognition of an appropriate mating partner and the achievement of fertilization, reproductive isolation follows per definitionem. In our view a biosemiotic approach clearly helps to identify those relevant structures. Especially when behavioural or physiological traits are unavailable decision processes would benefit from a biosemiotics-based species delimitation approach as a new source of data within the multidisciplinary undertaking of modern integrative taxonomy (Dayrat 2005; Řezáč et al. 2014). Thus, biosemiotics contributes to restrengthening morphology and to counteracting its severe decline that has started in the twentieth century.

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