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GENITALIC POLYMORPHISM—A CHALLENGE FOR TAXONOMY

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ABSTRACT. Genitalic polymorphism (including polymorphism of secondary sexual characters) is a typical example of a phenomenon that found no place in taxonomy as there was no framework to place it. Neither the speciation models used in ecology nor the species concept currently in use with taxonomists ‘‘allowed’’ species to have discontinuously polymorphic genitalia. Recent developments in ecological modeling that make sympatric speciation acceptable, and changing ideas about sexual selection, both imply genitalic polymorphism in particular circumstances. According to the mate check hypothesis the presence of hidden but crucial new adaptive characters is checked during courtship and mating. Sympatric speciation with changing behavioral characters without shifts in somatic traits, goes through a phase of intraspecific polymorphism during which the mating module obtains new traits backing up the newly acquired hidden character. It implies that this speciation process ends with the alteration of the recognition module. After the completion of the speciation process, cases of atavism with loss of behavioral adaptations through deleterious mutations or reversions and reappearance of ancestral genital characters, are expected to occur regularly. Without these, the mate check mechanism would be meaningless. A number of examples of both types of genitalic polymorphism in arachnids are presented. It explains why genitalic polymorphism is rarely observed although it might be a common phenomenon.

Keywords: Atavism, female choice, mate check, sexual selection, species concept, relapse, teratology

So far, aberrant specimens have been considered a rare phenomenon and the result of unusual ‘‘mistakes’’ of nature. The statement of Sorkin (1982) is symptomatic of the general attitude towards these occurrences: ‘‘. . . anomalies and teratologies do occur naturally and the taxonomist should be aware that species have been described from these freaks of nature . . . ’’. Specimens with deviating morphology have indeed often been called teratologies almost by definition. Yet, there is a clear difference between polymorphism and teratology. The latter phenomenon is morphologically characterized by asymmetry and uniqueness. If large numbers of teratologies are studied (Mitov 1995; Curcic et al. 1995) similar or identical cases may be found but these must be considered as the inevitable result of chance. Polymorphism on the other hand has a genetic origin and has been defined by Ford (1953) as follows: ‘‘The occurrence together, in the same habitat, of two or more discontinuous forms of a species, the rarest of which is too frequent to be maintained merely by recurrent mutation.’’ So teratology and polymorphism are vastly different phenomena.

As intraspecific polymorphism, and genitalic polymorphism in particular, cannot be dismissed as natural errors, their occurrence has long been problematic. The reason for that is the general application by taxonomists of the phylogenetic species concept. This concept defines species as ‘‘the smallest diagnosable sample of self perpetuating organisms’’ (Wheeler & Platnick 2000) which these authors argue to be the only workable concept to date. This species concept, together with the dismissal of sympatric speciation (Coyne 1992; Rice & Hostert 1993), prevented a sound interpretation of the rare cases in which genitalic polymorphism was observed, sometimes as a spin-off from research involving a breeding program. Yet, in some exceptional cases, certain researchers have accepted that a polymorphic phase in speciation exists (Tabachnik et al. 1979; Emberton 1995) but so far no such explanations have been reported in arachnology. Now that the concept of sympatric speciation gains adherents and has become much more acceptable thanks to recent models (Kondrashov & Kondrashov 1999; Dieckmann & Doebeli 1999, referred to as the KK and DD models by Tregenza & Butlin

1999) even taxonomists subscribing to the phylogenetic species concept reckon with the occurrence of polymorphism (Wheeler & Platnick 2000).

Predictions of the mate-check hypothesis, formulated for the first time by Jocqué (1998) and detailed in Jocqué & Szûts (2001), do expect genitalic polymorphism to occur during the process of speciation as well as after the completion of the process through a phenomenon here referred to as ‘‘relapse’’, which is a particular type of atavism. The present paper is a purely theoretical essay that aims at cornering the framework in which both genitalic polymorphism with more or less stable incidence and the occurrence of rare specimens with aberrant genitalic characters, so far considered as ‘‘teratologies,’’ can be placed.

MATING AND RECOGNITION MODULES

It is accepted (Eberhard 1996) that the timing of the female decision about what male or what sperm will be selected for egg fertilization, varies to a large extent from one species to the other. In many species the choice occurs before proper mating and is then called ‘‘overt choice’’ whereas in many others the selection is made after copulation, a phenomenon called ‘‘cryptic choice.’’ As a consequence, the decision may be dependent upon a wide array of possible signals emitted by the male. The most common signals are apparently tactile and are emitted during mating itself. These are emitted by the genitalia or secondary genitalic structures. In many animals though, the crucial information may be transmitted by visual (mating dances), auditory (stridulation) or chemical (pheromones, gustatorial) types of courtship, often by combinations of two or more of these, but before mating takes place. In order to facilitate the discussion about the many aspects that may be involved in the transfer of information during courtship and mating, we introduced the term ‘‘mating module’’ which encompasses all the means by which information is exchanged (Jocqué & Szûts 2001).

In analogy, the term ‘‘recognition module’’ is here introduced. It concerns the mechanisms for exchange of the information that enables individuals to recognize conspecifics. On average the recognition module tends to be much smaller than the mating module and is emitted to a similar extent by both sexes. It enables possible partners to quickly recognize the identity of a partner before they engage in time and energy consuming proper mating. Pheromones in general and pheromone impregnated silk (Tietjen & Rovner 1982; Jackson & Cooper 1990; Pollard et al. 1987) are excellent examples of such modules in spiders.

THE MATE CHECK HYPOTHESIS

Students of the niche theory differ in their views on speciation from those who study sexual selection. Adaptation to, and shifts in ecological niches are paramount with the former (e.g., Southwood 1978), rapid evolution of *s*exual *c*haracters (SC, including secondary sexual characters), supposedly molded by female choice, are more important for the latter (see Andersson 1994, for a review). One of the reasons for these unrelated or even opposite views is that in some speciose taxa, e.g. *Hortipes* Bosselaers & Ledoux (Bosselaers & Jocqué 2000), *Storena* Walckenaer (Jocqué & Baehr 1992), *Diores* Simon (Jocqué 1990), the only morphological differences between species appear to be in the SC. This might give the impression that speciation has occurred without the development of adaptive novelties other than improved stimulation of the female (Eberhard 1985, 1994, 1996) or as a result of sexual conflict (Parker & Partridge 1998; Arnqvist 1998; Arnqvist et al. 2000). Therefore the cause for speciation is sought in the evolution of these SC alone and female choice is assumed to be the driving force behind speciation. In these hypotheses, abstraction is made of behavioral or other hidden adaptations which may be subject to profound changes but often have no bearing on somatic morphology. The weakness of these hypotheses is that they do not have an explanation for the persistence of the species with less complex genitalia.

The ‘‘mate check’’ hypothesis on the other hand links elements of the theories of the ‘‘niche’’ and ‘‘sexual selection’’ (Jocqué 2000) and assumes that evolution through behavioral adaptation, allowing more efficient use of underexploited resources, is backed up by changes in the mating module. The presence of these crucial characters is checked, hence ‘‘mate check,’’ during courtship and mating. This line of thinking may explain the

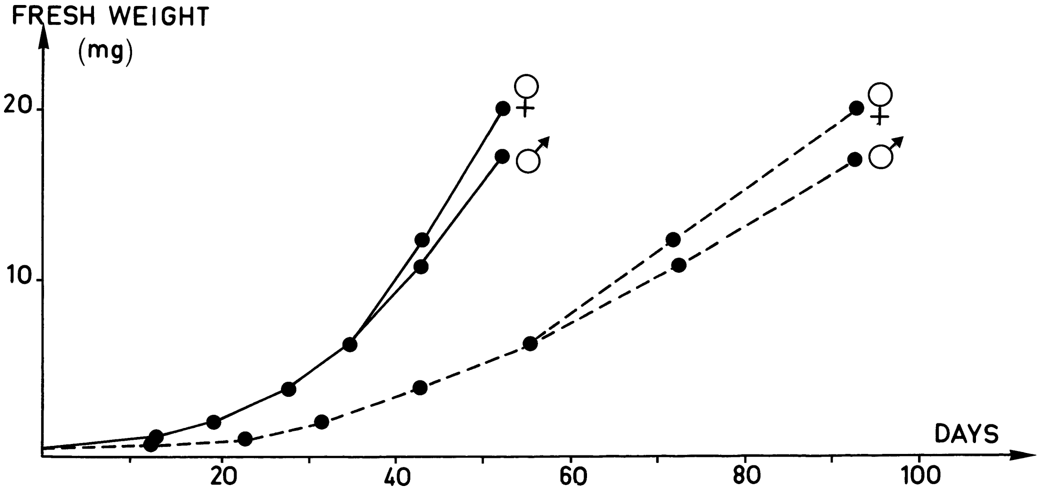

Figure 1.—Development rate of spiderlings of *Pardosa injucunda* hatched from a single egg case; remarkable is the occurrence of two well separated cohorts of which the fastest needs almost only half as much time as the slow cohort to reach adulthood (after Célérier, 1981).

large range of complexity of SC in closely related and somatically often indistinguishable taxa, implying that complexity of SC is linked to ecological specialization. It also predicts that in the case of a speciation event, the original species persists in what is called the source (optimal habitat) whereas the newly evolved species thrives in the sink (marginal habitat) thanks to a new adaptation.

The core of the ‘‘mate check’’ hypothesis is a mechanism that guarantees gamete exchange with a partner that possesses recently acquired behavioral or other hidden characters. The need for such a mechanism is based on the observation that losses of new adaptations through deleterious mutations are remarkably high (Gould & Lewontin 1979; Lande 1994) . Hidden adaptations are often nothing else than preference for a particular microhabitat and these differences are obviously difficult to demonstrate, certainly when they are present within a single, albeit polymorphic, population. Different habitat preference has been shown though for conspecific morphs of certain Lepidoptera (Jones et al. 1993), Diptera (Tabachnik et al. 1979) and fishes (McPhail 1964). Hawthorne & Via (2001) showed that there is genetic linkage between ecological specialization and reproductive isolation through host choice in pea aphids. In populations without polymorphism but in which the first step to speciation has occurred, the new adaptation is even more difficult to show. An excellent example of a hidden character in spiders is found in Célérier (1981) who reports on the breeding results for the west African lycosids *Brevilabus gillonorum* Cornic 1980 and *Pardosa injucunda* O.P.-Cambridge 1876 (Fig. 1). In both species, spiderlings from the same egg cocoon were found to grow at very different rates and to form two clearly separated cohorts. *Pardosa injucunda* reached adulthood either after 50 days for the fast cohort or after 100 days for the slow one. The fast development can be considered an adaptation to marginal habitats or periods where the rainy season is shorter than in the optimal condition, in which a development time of 100 days is fast enough. Slow development has the advantage that the life cycle can be completed efficiently even when prey is scarce (Jocqué 1983). But as there is not the slightest morphological difference between the two groups, this adaptation must be considered as ‘‘hidden’’.

SYMPATRIC SPECIATION UNDER THE MATE CHECK MECHANISM

The mate check hypothesis clearly assumes sympatric speciation, a speciation model that has gained support in recent literature. Especially the ‘‘KK’’ and ‘‘DD’’ models (see above) stress the occurrence of a polymorphic phase of genitalic characters and the fact that speciation needs changes in multiple loci. In our diagram (Fig. 2) these changes are repre-

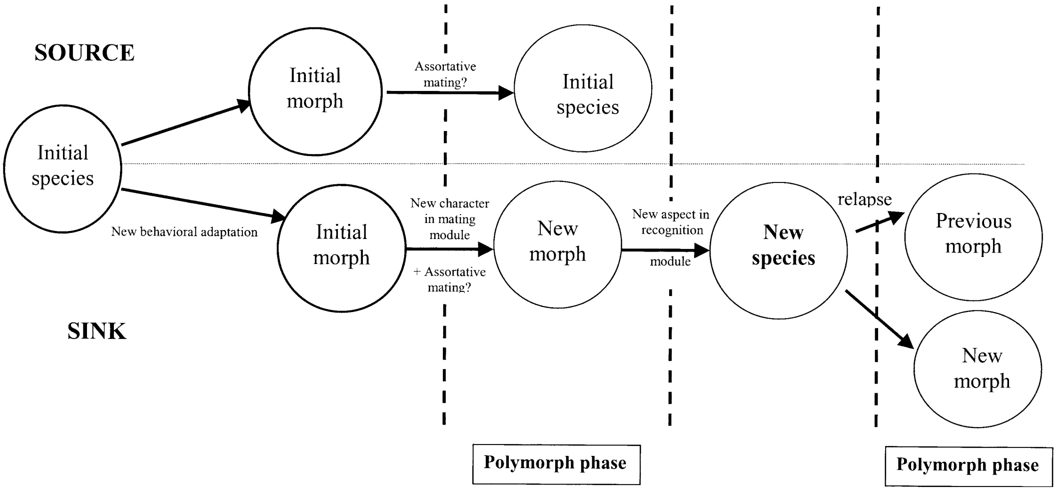

Figure 2.—Diagrammatic model of sympatric speciation according to the mate check hypothesis. Part of a population is able to breed successfully in a former sink thanks to the acquisition of a new, hidden adaptation, later backed up by a new character in the mating module. Assortative mating might not be necessary as there is disruptive selection as a result of the distorted survival rate in the source and sink subhabitats; in the former sink, mate check will further reduce the breeding success of specimens that do not have the new linked characters. Speciation is completed by the modification of the recognition module. The initial or an atavistic morph may reappear due to relapse (deleterious mutations or reversions) eliminating the behavioral adaptation and its linked trait in the mating module. It should be noted that two phases of genitalic polymorphism are expected.

sented by a new adaptive trait, a new trait in the mating module and a modification of the recognition module.

Polymorph phase.—The hypothesis coincides well with the findings of Rice & Chippindale (2001) who state that sex may play an important role in consolidating beneficial mutations as suggested in Jocqué (1998).

The reason for the chronology of the sequence—new behavioral character—new aspect of mating module—modification of recognition module, has to do with the observation that the morphology of the genitalia themselves does very often not prevent copulation and that, in many cases, if not all, recognition takes place before copulation or courtship commences (Jackson 1987; Jackson & Cooper 1990; Pollard et al. 1987) sometimes even before the sexes meet. This observation may even lead to a new species concept which defines a species as “a population whose members share a unique recognition module”.

The mate check mechanism only makes sense if there is a real risk for mating with a partner that has lost a critical hidden adaptation and together with it the linked aspect in the mating module. This means that we must expect to come across specimens, males as well as females, that have a mating module, which in many cases means sexual organs, differing from what is found in “normal” specimens and which we will call “relapses.” Since the differences must be discontinuous, it should be very easy to recognize these specimens. Yet, the present habit to define species exactly on the base of discrete differences, not linked by intermediates in a morphocline, has prevented the detection of relapses. It is therefore likely that the specimens with relapse that have reached adulthood and have been found, are hidden in the literature as separate species!

EXAMPLES OF POLYMORPHISM

Pre-speciation polymorphism.—Although many cases of assumed incipient speciation in sympatry have been reported, very few examples mention the combined change of behavior and morphology in conspecific morphs. The few studies mentioned above and those of Müller (1957) on *Euscelis* (Homoptera) and Meyer (1989) on *Cichlasoma citrinellum* (Pisces) are among the few exceptions. But if sympatric speciation is as common as assumed by some authors (Tregenza & Butlin 1999) we may be surrounded by a multitude of polymorphic species in the course of speciation, of which the different morphs are considered as heterospecific. A perfect example is the case of *Oedothorax gibbosus* (Blackwall 1841) and *O. retusus* (Westring 1851)(Linyphiidae) that have been described as different species on the basis of discrete differences in the shape of the male carapace (see Table 1). Although they were already suspected to be conspecific by Simon (1926) they were only proven to be so by De Keer & Maelfait (1988). Maelfait *et al.* (1990) and Heinemann & Uhl (2000) further specified the details of this case of polymorphism. Van Acker et al. (2002) recently found that the morphs have different ecological optima that are congruent with the predictions of the hypothsesis. Another case is that of *Pelecopsis janus* Jocqué 1984 (Linyphiidae), a spider species with dimorphic males from South Africa. These male forms were described in the same species as the samples only contained one type of female and the male palps of both forms are identical (Jocqué 1984). *Troxochrus scabriculus* (Westring 1851) and its form *T. scabriculus cirrifrons* (O. P.-Cambridge 1871) are another example of dimorphic males (Müller 1984). Recently Huber & Gonzalez (2001) described the new species *Siboneya anthraia* Huber & Gonzalez 2001 (Pholcidae) in which the conspecific female morphs, obtained in a breeding program, have different epigynes. Other possible candidates for dimorphic females are *Drassodella vasivulva* Tucker 1923 and *Drassodella septemmaculata* Strand 1909, described as separate species by Tucker (1923) from the Cape in South Africa. The male of the second species is still unknown. Yet large pitfall samples only contain one male form and high numbers of both female forms. Since males of ground spiders are without exception always more abundant than females in pitfall samples, it is assumed that the somatically identical females of these *Drassodella* species are conspecific (Jocqué, pers. obs.).

These few examples prompt the following reflections: the detection of polymorphism is either based on male secondary sexual characters (male carapace shape) or female characters. In all these cases, the identity of the male, based on its palpal characters that are supposed to be the final criterion for species diagnosis, has given rise to the initial suspicion that one was dealing with polymorphic species. But if different males were found with very similar or identical females, these would be cataloged as different species without hesitation. The following questions arise: Do males with polymorphic copulatory organs occur and if so, how frequent are they? Are there species in which both females and males are polymorph? And does this kind of polymorphism indeed represent a stage in sympatric speciation?

Post-speciation polymorphism, atavism or relapse.—Appearance of rare aberrant forms are usually dismissed as teratologies. Yet, rare aberrant specimens, when symmetrical, do not fit the definiton of teratology nor that of polymorphism (Ford 1953). For that reason we here adopt the term ‘‘relapse,’’ defining a type of atavism that implies loss of an aspect of the mating module together with a hidden adaptation.

Very few cases of apparent relapses are known most probably because the conditions to find them were not available. One of the most spectacular cases is that of *Bryantella smaragdus* (Crane 1945) (Scioscia 1995 and figures therein). This author raised spiderlings from egg batches produced by females collected in the wild. Among the offspring from one cocoon she found no less than four types of somatically identical males with palps with discontinuous differences mainly in the length of the embolus and the shape of the tibial apophysis. Three types of females with discontinuous differences in the epigyne were obtained. Each of the morphs was represented by several specimens. The phenomenon was observed in the offspring obtained from several cocoons. According to the presently prevailing custom in spider taxonomy, the extremes, with, as the most spectacular difference, the length of the embolus, would be placed in different genera. One of the less spectacularly aberrant morphs, collected in the wild had indeed been described in a different genus. Chickering (1946) described the new species *Parnaenus convexus* which now appears to be one of the morphs of *Bryantella smaragdus* (Scioscia 1988). Yet, in the same paper Chickering describes another species of *Bryantella* but did thus not realize these species were very closely related. It is important to note that the morph described by Chicker-

Table 1.—Overview of cases of genitalic polymorphism and specimens with aberrant genitalic characters in spiders.

Taxon	Number of morphs	Sex and number involved	Characters involved	Situation	Source
Pre-speciation polymorphism					
Oedothorax gibbosus (Blackwall 1841)	2	M	cephalothorax shape	synonymy with *O. tuberosus* shown by breeding	De Keer & Maelfait 1898; Maelfait et al. 1990; Heinemann & Uhl 2000
Pelecopsis janus Jocqué 1984	2	M	cephalothorax shape	suspected intraspecific polymorphism	Jocqué 1984
Troxochrus scabriculus O.P.-Cambridge 1851	2	M	cephalothorax shape	suspected intraspecific polymorphism with *T. s. cirrifrons* (O.-P. Cambridge 1871)	Müller 1984
Drassodella septemmaculata (Strand 1909)	2	F	epigyne	suspected conspecific with *D. vasivulva* Tucker 1923	unpublished
Siboneya anthraia Huber & Gonzalez 2001	2	F	epigyne	polymorphism shown by breeding	Huber & Gonzalez 2001
Relapses					
Pardosa amentata (Clerck 1757)	2	5 M	male palp	described as f. *ileachensis* of *P. amentata*	Beaumont 1991
Pardosa palustris (L. 1758)	3	2 F	epigyne	recognized as aberrant conspecific	Bergthaler 1997
Pardosa agrestis (Westring 1861)	3	F	epigyne	recognized as aberrant conspecific	Samu (pers. comm.)
Bryantella smaragdus (Crane 1945)	4	17 M	male palp	1 morph described as *Parnaenus convexus*	Scioscia 1988, 1995
Bryantell asmaragdus (Crane 1945)	3	22 F	epigyne	1 morph described as *Parnaenus convexus*	Scioscia 1988, 1995
Bacelarella tentativa Szûts & Jocqué 2001	2	2 M	male palp	described as separate species, suspected relapse of *B. conjugans*	Szûts & Jocqué 2001
Bacelarella pavida Szûts & Jocqué 2001	2	4 M	male palp	described as separate species, suspected relapse of *B. conjugans*	Szûts & Jocqué 2001

ing was found in Panama, whereas the females used by Scioscia came from southern Brazil. The differences between the morphs are strictly discontinuous and no intermediates linking the different morphs were found. No differences in behaviour between the different morphs were observed.

Aberrant symmetrical spiders, most often males, have been encountered in the wild and either treated as different species as in the case of *Bryantella*, as separate ‘‘form’’ (*Pardosa amentata* f. *ileachensis,* Beaumont 1991) or as enigmatic morphs in *Pardosa palustris* (L. 1758) (Bergthaler 1997) and *Pardosa agrestis* (Westring 1861) (F. Samu, pers. comm.). In each of these cases, several specimens were found, either in the same population or far apart. The differences from the typical morph were always discrete.

According to the mate check hypothesis, similar cases should be common, at least in somatically stable taxa with a wide range of variation in the genitalia. For two reasons the chance to detect such morphs is fairly small. First of all these morphs are likely to be rare. As the loss of a genitalic trait is supposed to imply the loss of a crucial behavioral (hidden) character, it is to be expected that only in unusually favorable circumstances, will the specimen with relapse reach adulthood. Second, we do not expect species to be polymorphic at least not in such a way as to present clearly discontinuous differences. Scanning the literature of revisions and faunas, one comes across quite a number of ‘‘rare species’’ that have been described on one or a few specimens, often of one sex and found among numerous specimens of a related species. In the present context it is not an exaggeration to suggest that the identity of such species should be controlled.

The case of *Bacelarella* Berland & Millot 1941 illustrates this. In rain forest in Ivory Coast, seven syntopic species of litter dwelling salticids belonging to the genus *Bacelarella* (Szûts & Jocqué 2001) were found. They are somatically very similar and apparently adapted to life in the poorly lit forest floor environment. They represent an amazing morphocline with increasingly complex genitalia (Jocqué & Szûts 2001), the most simple ones are very rare and respectively two and four specimens have been collected in a two year pitfall sampling campaign combined with sticky traps, sweeping and hand collecting. The position of both of these species on a cladogram (unpublished) as derived from a species with more complex genitalia, strengthens the suspicion that these might be relapses of the ‘‘ancestral’’ species.

The chance to come across these specimens is less remote in a laboratory breeding program. The artificial circumstances encountered in the laboratory may be considered as ecological relaxation. Even specimens with reduced fitness as a result of the loss of adaptive characters may be able to reach adulthood in such a situation. That these cases have even been overlooked in laboratory breeding programs, is not surprising either. Since one expects animals from the same parents to have the same diagnostic characters, these characters are usually not verified. It is taken for granted that they are all the same. As a control will most often need detailed observation of genitalia, it is not evident that differences, albeit discrete, are detected, unless the program is especially set up for that purpose.

Although genitalic polymorphism is only rarely observed, the cases that are presented here might be examples of two phenomena that are not rare at all: prespeciation polymorphism and relapse.

The only way we can find the answers to these questions is to look back to the past and try to find out how many species have been described on conspecific polymorphic morphs. It is evident that this will not be a simple process and that in many cases either a breeding program or molecular analysis will be needed to obtain the answer.

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