

Rapid evolution and species-specificity of arthropod genitalia: fact or artifact?

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Abstract

It is widely accepted that there is compelling evidence in the taxonomic literature that in many animals with internal fertilization the genitalia (and functional equivalents) evolve more rapidly and are species-specific to a higher degree than non-genitalic features. In this article, a series of biases and constraints inherent in traditional taxonomic practice are discussed that might be partly responsible for the two phenomena: (1) Emphasis on non-genitalic characters for grouping of species and higher taxa; (2) Emphasis on qualitative differences in species-level taxonomy; (3) Extrapolation from non-dimensional situations to allopatric populations; (4) A priori assumption of species-specificity of genitalia; (5) Low numbers of available specimens for most species. It is concluded that both traditional and modern methodological approaches (such as analysis of variation and analysis of character evolution based on DNA sequence data), coupled with an increased awareness of these potential problems, are necessary to evaluate objectively the commonality of rapid evolution and species-specificity of genitalia.

Key words: rapid evolution, species-specificity, genitalia, polymorphism, taxonomic biases, constraints

Introduction

Relatively rapid evolution (in relation to other traits) and species-specificity are widely seen as the hallmarks of genitalic morphology and evolution. This implies that we are essentially dealing with facts, with something we need not question any more, and ultimately with something on which we can design experiments, formulate hypotheses, and develop new explanatory ideas. It is telling that Eberhard (1985), in the most comprehensive treatment of genitalic evolution, needs just a few sentences to introduce these phenomena. As to species-specificity, he states that “it has long been recognized ... that in a variety of animal groups, genitalia are especially useful in distinguishing closely related species” (op. cit.: 1). As to rapid evolution, he concludes that “the fact that taxonomists can often find greater differences between related species in genitalia than in other structures implies that relative to the other structures the genitalia have diverged rapidly” (op. cit.: 2–3). Actually, the entire first chapter is used to illustrate these statements and

to document the wide range of animal phyla in which they seem to apply, but the real “aim of this book is to answer the question of why this is so” (op. cit.: 1), not to question the reality of the two phenomena.

I anticipate that the conclusion will not be that this is all wrong. A growing amount of both empirical data and mathematical models supporting rapid evolution of traits and proteins related to fertilization (e.g. Howard & Berlocher 1998, Gavrilets 2000) indicates that these are in fact important phenomena. The point here is that these phenomena may not be as “near universal” as Eberhard proposes in his book and as others have assumed in their work (e.g. Alexander et al. 1997, Arnqvist et al. 1997, Arnqvist 1998, Jocqué 1998). The assumption of the reality of rapid evolution and species-specificity rests primarily on evidence from the taxonomic literature, and I will argue that this evidence is biased and not compelling.

This article is not about exceptions. Almost any good biological rule has exceptions, and exceptions to the present phenomena have long been known and discussed

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(e.g. the entire ninth chapter in Eberhard's book). In this sense I disagree with Hausmann (1999) who views the occurrence of genitalic polymorphism in one clade of moths as a falsification of the 'rule' of species-specificity. Instead, this article is about possible alternative reasons for why the taxonomic literature could lead (or mislead) us to the conclusion that, in general, genitalia evolve relatively rapidly and are species-specific. Basically, there are two extreme alternatives (and anything inbetween): either, genitalia do indeed evolve faster than other structures and are indeed species-specific to a special degree, and taxonomists have discovered this. Or, genitalia are not special in these regards, but taxonomists' concepts, methods, constraints in practical work, etc. have misled us to believe that they are. What I will suggest is that such biases do exist in traditional taxonomic work.

The examples used in this article are almost exclusively taken from one family of spiders, the daddy long-leg spiders, or Pholcidae. The reason is not that these animals are somehow special. To the contrary, I suppose that they are not, and that the arguments presented in this article are valid for most kinds of sexual organisms with internal fertilization. I see no evidence supporting the idea that taxonomists of other groups (at least arthropod groups with internal fertilization) differ in their traditions and practices in a way that would seriously narrow the significance of the problems discussed. The reason I chose pholcids to illustrate my points is that this is the group I have studied for several years, mainly with respect to their reproductive biology, taxonomy, and phylogeny (see Huber 2000, 2001 and references therein).

Rapid evolution

Methodological bias

If genera and higher categories are predominantly defined by non-genitalic characters (e.g. Platnick 1975), then genitalic diversity could partly result from the non-monophyly of taxa based on characters other than genitalia.

In other words, if species with interspecific variation in genitalia and non-genitalia are grouped according to non-genitalic characters, then if the resulting groups are not monophyletic, non-genitalic characters will necessarily appear to evolve more slowly than genitalia. Figure 1 shows two pholcid species from Colombia that illustrate this point, and that represent one of many examples suggesting slow genitalic evolution as compared to non-genitalic characters. If these species were grouped according to traditional criteria (e.g. shape of prosoma, positions of eyes, etc.), they would end up in different genera. However, the genitalia are extremely similar in several aspects, and the procurus (one of the parts that

are inserted into the female during copulation) shows a specific design that is known only from western Colombia (strongly curved; spine plus membrane). This geographic closeness (rather than just the morphological similarity) strongly suggests that the two species are in fact close relatives, and that certain non-genitalic characters have evolved much more rapidly than the genitalia.

The question is, how often does it happen that species which are not closely related are grouped according to overall similarity? Is this only a result of bad taxonomic practice, a problem that can be largely solved by modern revisions and phylogenetic analyses, and by modern methods that are able to detect homoplasy? The refractory character of the problem is well known to anybody doing phylogenetics, and is here illustrated by one of the traditional subfamilies of Pholcidae, the Ninetinae (Fig. 2). These are tiny spiders (mostly about 1–3 mm total body length) that share, apart from their size, a number of characters: short legs, few tarsal pseudosegments, globular pro- and opisthosoma, relatively large anterior median eyes, etc. And, importantly, they also seem to share the habitat: in contrast to 'usual' (i.e. long-legged) pholcids, they all seem to have been collected in the interstices of the soil, in leaf litter, and under stones. In contrast to this overall similarity, the genitalia are highly diverse, with only a few scattered similarities among each other and to other pholcids. It is thus not surprising that cladistic analysis based on morphology resolves Ninetinae as a monophyletic group (Huber 2000, 2001). However, the present example illustrates two fundamental problems that are well known but have apparently never been discussed in the context of genitalic evolution:

(A) In phylogenetic analysis characters are treated as if they were independent (e.g. Kitching et al. 1998, Hillis & Wiens 2000). In ninetine spiders there is presently no evidence to the contrary, but it is easy to imagine a plausible story about two or more clades of 'usual' pholcids adapting to the conditions in interstices convergently, and thus developing certain characters convergently (short legs, globular body parts, few tarsal pseudosegments, etc.).

(B) Obviously, cladistics only works with characters that can be coded into a matrix. As mentioned above, there are indeed certain similarities between the genitalia of certain Ninetinae and those of certain genera of 'usual' pholcids. However, the similarities are rather vague, not difficult to illustrate but difficult to describe in words, and almost impossible to code unambiguously into a matrix that reduces complex shapes and relationships to a simple and discrete alphanumeric format.

It is such vague similarities and plausible but unconvincing stories that most cladists justifiably reject as grouping criteria. However, this removes neither the po-

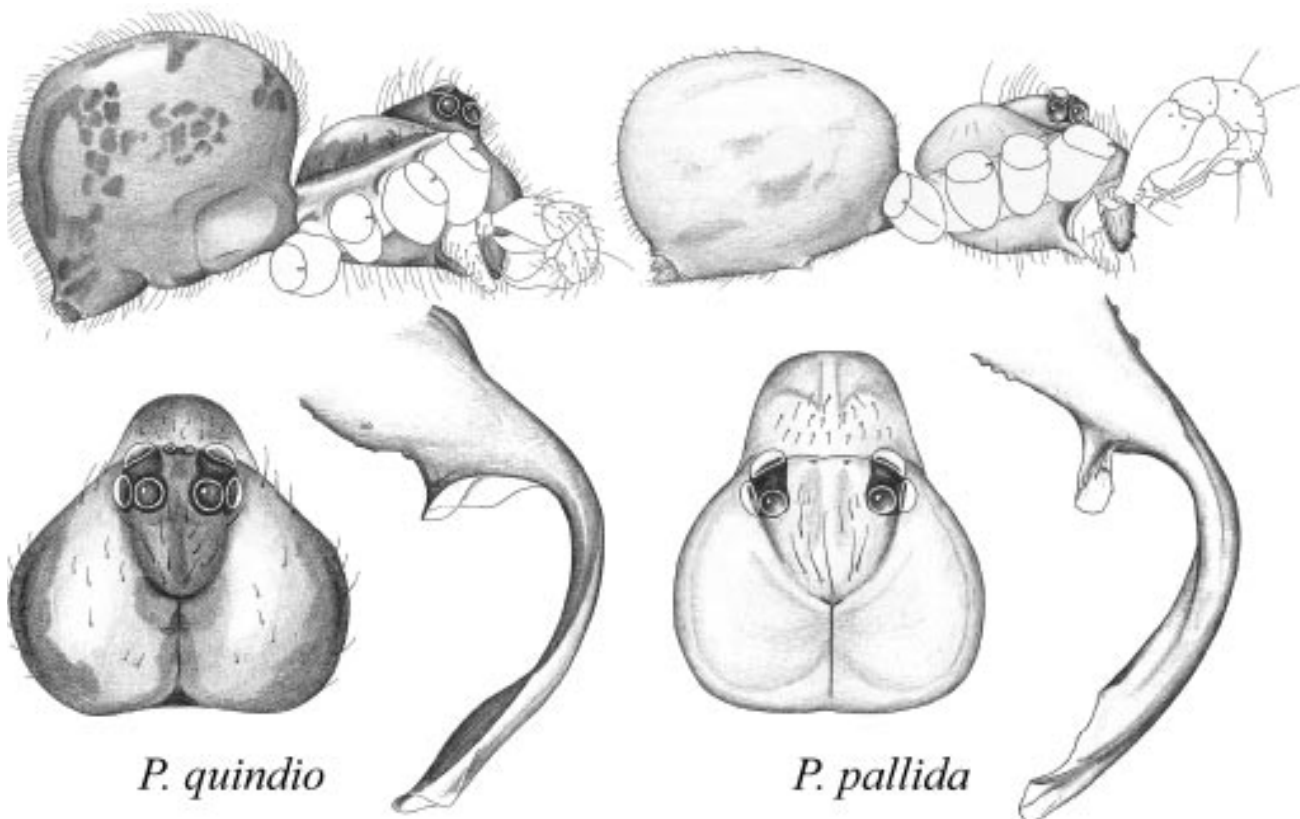


Fig. 1. Two species of the Colombian pholcid genus *Pomboa* Huber. Note the conspicuous differences in overall shape, prosoma shape, and eye pattern. The genitalia, however (here represented by the procurus, i.e. the structure that is inserted into the female and is usually the most diverse), are almost identical, with this specific shape present exclusively in western Colombia. Adapted from Huber (2000).

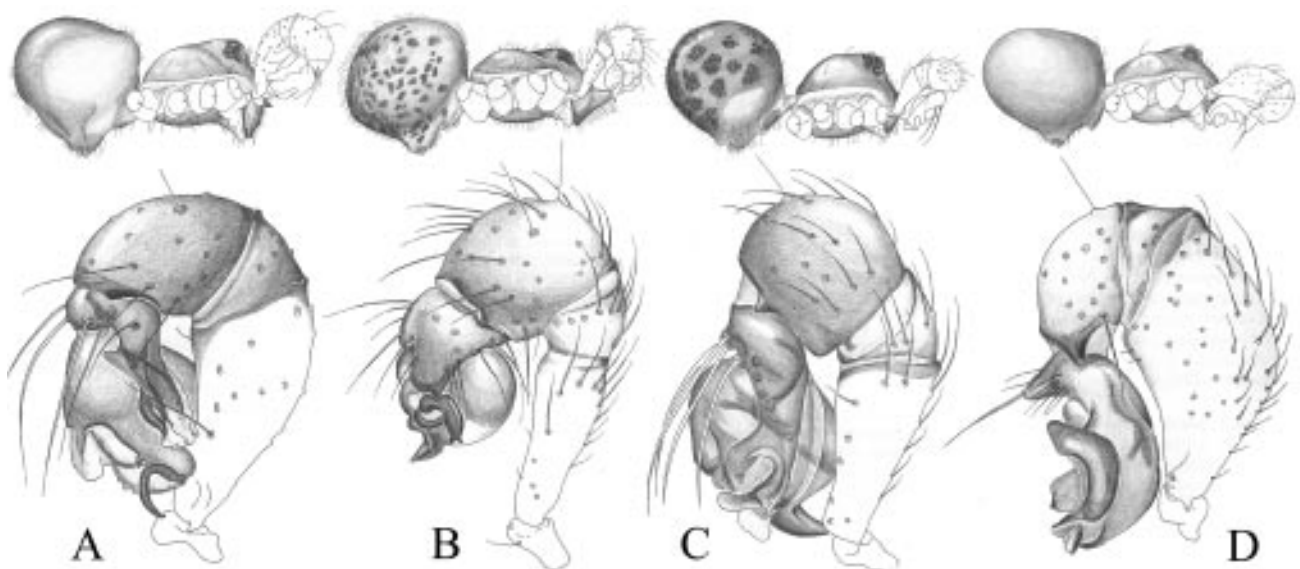


Fig. 2. Four species of the pholcid subfamily Ninetinae. A. *Aucana kaala* Huber, 2000. B. *Papiamenta savonet* Huber, 2000. C. *Guaranita goloboffi* Huber, 2000. D. *Chisosa diluta* (Gertsch and Mulaik, 1941). Note that the spiders look very much alike overall (and they share additional characters like short legs, eye pattern, etc.), but the genitalia (here represented by the left male palps) are extremely diverse. Adapted from Huber (2000).

tential problem of correlated characters (cf. Hillis et al. 1996: 410), nor the problem of subjectivity of character choice that is partly governed by our ability or inability to code certain characters. The idea that “only illustrations, photos or, above all, drawings, provide the way to describe, analyze and communicate these [morphological] data” (Pierre 1992) may be inconvenient for phylogenetic analysis but a reality nevertheless.

Modern phylogenetic methods do not a priori assign different weights to different character systems like genitalia and non-genitalia and should thus not be influenced by this bias. However, biases in initial character choice and the problem of character independence mean that cladistics does not automatically insure against the fallacies of overall similarity (i.e. homoplasies). A potential way out of the problem is to have a phylogeny produced on the basis of other (non-morphological) evidence, most obviously DNA sequence data. As molecular data may provide solutions to several of the problems discussed in this article, this topic is taken up again at the end of the paper.

Perceptual bias

If interspecific differences tend to be qualitative (i.e. non-overlapping) in genitalia, but quantitative (overlapping) in non-genitalia, then taxonomists may prefer and emphasize genitalia for practical reasons alone, and

quantification of phenotypic change (‘rapid’ versus ‘slow’ evolution) becomes (nearly?) impossible.

Putting aside philosophical questions about the distinction between qualitative and quantitative, such as those addressed by Thom (1996) or Stevens (1991), it suffices to say that I follow the common use of these terms as synonyms for overlapping and non-overlapping ranges (Kitching et al. 1998). The practical reasons for taxonomists’ preference of characters that differ qualitatively are that “quantitative characters are difficult to describe fully, requiring means, medians and variances to establish the gaps” (Kitching et al. 1998: 20).

For the sake of simplicity, this point is here illustrated with a hypothetical example, derived from pholcids of the genus *Mesabolivar* Gonzalez-Sponga. Assume that a taxonomist has three samples of organisms that show several differences in non-genitalic characters but only one difference in the genitalia (Fig. 3). Consider the following two scenarios:

(A) The taxonomist has good statistical samples (at least 15–20 individuals in each sample) and the time and inclination to do statistics on them (improbable assumptions; see below). The taxonomist will very probably find that the non-genitalia show overlapping ranges of the variables measured, whereas the genitalia do not. The taxonomist may find that non-overlapping ranges can also be found in non-genitalia by using ratios, but the question is: which characters will he/she use in the

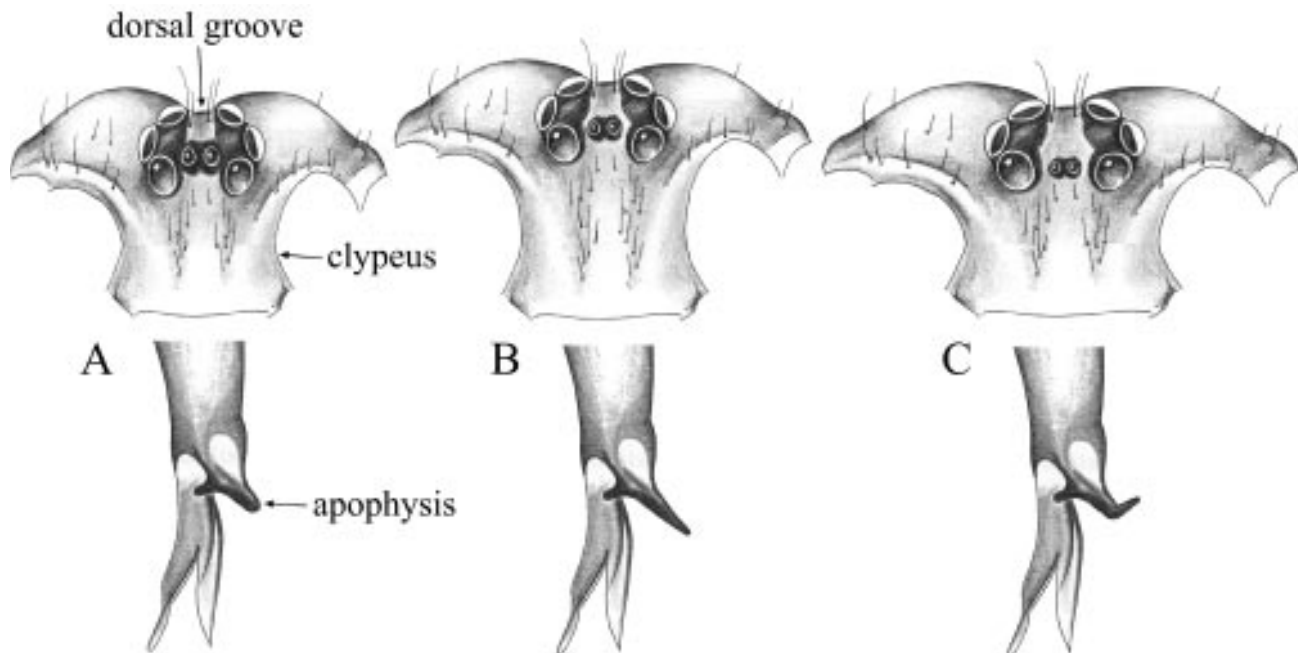


Fig. 3. Three hypothetical species of pholcid spiders, simplified from representatives of the South American pholcid genus *Mesabolivar* Gonzalez-Sponga, that show several quantitative differences in the prosoma (distance between lateral eye triads, position of anterior median eyes, depth of dorsal groove, width of clypeus, etc.), but only a single qualitative difference in the genitalia (shape of one apophysis).

diagnoses, in identification keys? And, most importantly, which characters will be illustrated, and thus strike the fellow biologist as being somehow special? Very probably the genitalia, even if they show fewer differences (as in the present example).

(B) The taxonomist has only a few individuals in each sample (which is the usual case; see below). In this scenario, he/she will tend to choose the genitalia a priori, if only for the simplicity of diagnosing taxa by qualitative differences.

This example implies the unproven assumption that the evolution of genitalic rather than non-genitalic characters tends to produce qualitative differences. As such, the assumption will probably sound plausible or even obvious to most systematists actively working on alpha taxonomy, and it agrees with the fact that genitalic structures are often more difficult to homologize than non-genitalic characters (e.g. Coddington 1990 on spiders). Proof will not come easily, but the assumption can be tested by large-scale morphometric studies of organisms whose phylogeny is well established.

Species-specificity

Extrapolation from 'non-dimensional' situation

If the clear-cut genitalic differences among sympatric, synchronic (i.e. non-dimensional sensu Mayr 1955) species are used as a yardstick for allopatric and allochronic populations, then 'genitalic polytypisms' are almost impossible to discover.

It is usually quite easy to distinguish the species at one place and one time. In this non-dimensional situation, genitalia have proven to be of exceptional value to taxonomists in many animal groups. The old impression that genitalia vary intraspecifically less than non-genitalia was partly supported by a recent morphometric analysis of several insect and spider species (Eberhard et al. 1998). These authors found that even though the coefficients of variation showed only a tendency to be lower in genitalia than in non-genitalia, genitalia consistently had lower slopes in regressions on indicators of body size. To allow comparisons among species, each species in that study was represented by a single population (actually by a non-dimensional fragment of a population). However, the term species-specificity is about species, and species have a spatial (and temporal) distribution.

The point here is that traditional taxonomic publications often have a regional emphasis, and modern, taxon-based works often seem based on a species concept that worked fine in this non-dimensional situation (i.e., a typological species concept). In other words, we have found that genitalia are species-specific at one place, and when we find allopatric populations with

somehow different genitalia we conclude that we are dealing with a different species. This conclusion 'justifies' our original assumption of species-specificity, closing the logical circle.

In sum, species-specificity may be a fact in the non-dimensional situation, but extrapolating from regional patterns to species ranges – or, to use one of Ernst Mayr's favorite terms, to apply a yardstick developed in sympatric (and synchronic) situations to allopatric populations with differing genitalia – may not be appropriate. Using this yardstick makes it essentially impossible to discover species that are polytypic with respect to genitalic morphology. Two final points are noteworthy in this regard. First, most of the groups in which Mayr's concept of polytypic species has found wide support (birds, mammals, butterflies, snails; Mayr & Ashlock 1991) are (or were originally) not distinguished by genitalia. Second, a large percentage of known species are known only from single localities (e.g. 45% and 53%, respectively, in samples of beetle taxonomic papers cited in Stork 1993, 1997).

Theory prevents detection of genitalic polymorphisms

If species-specificity is assumed, polymorphisms are almost impossible to discover.

This point is similar to the previous, except that it is not about polytypic but about polymorphic species, that is, species that show discontinual variation within populations. The question is: how often are the morphs of one species described as different species? This question has been addressed recently in some detail (Huber & Pérez 2001b). We concluded that, even though we could find only a few cases of genitalic polymorphism documented in the zoological literature (Müller 1957, Kunze 1959 on cicadas; Inger & Marx 1962 on snakes; Ulrich 1988 on a fly; Mound et al. 1998 on thrips; Hausmann 1999 on moths; Huber & Pérez 2001a on spiders), there is no objective way to decide at this point whether these cases are just rare curiosities or more than that. 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 genitalic polymorphisms (actually polyphenisms) like those in *Euscelis* cicadas (Müller 1957, Kunze 1959) and in geometrid moths (Vitalieva 1995) may be quite common.

What we do know, however, is that several methodological and practical aspects of taxonomic work act together in a way that makes the discovery of genitalic polymorphisms very unlikely in the first place: (A) Species-specificity as a basic assumption, and the dominant role of genitalia in species identification; (B) The absence of data on the biology of the vast majority of in-

vertebrate nominal species; (C) The frequent use of extremely low sample sizes for species descriptions, resulting from the high frequencies of singletons and extremely low specimen numbers in museum collections. This last point is treated separately below because it has implications not only for polymorphisms but for the assessment of variation in general.

Numbers of specimens available

If most animals are known from a few specimens only, then most animals are not accessible to the evaluation of variation and polymorphism, and the question of species-specificity must be addressed using a much smaller sample of species than previously thought.

If most species are known from a few individuals from a single locality, then what general statements can be made 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 well-known fact that about the vast majority of 'known' species we know literally nothing (cf. Stork 1997). This is common knowledge, of course, but an objective quantification is difficult beyond the realm of a specialist's 'own' group.

Therefore, I shall here present two data sets that illustrate the point, but may or may not be representative for other invertebrates (a question that can only be decided by specialists for 'their' respective groups). The first set is about pholcids (Table 1). It gives a simplified but complete overview of the state of knowledge on the 787 nominal species known at this time (January 2002). The second set is a more or less arbitrary selection of taxonomic papers on spiders (Table 2). I cannot, and shall not try to, prove that this sample is representative for spiders. It is biased towards tropical taxa. However, I assume that by using large monographic works about specific families rather than scattered descriptions of new species, and by using rather recent publications, I will arrive at a conservative estimate.

The relevance of these numbers in the present context is the fact that a large percentage of organisms is known to science from a minimal number of specimens (for data on singletons in other taxa see Erwin 1997 and references therein). In the two samples, 33% and 49%, respectively, of the species are known from only one sex. From 40% and 55%, respectively, of the species fewer than four individuals are known, in most cases from a single locality (the higher percentages in Table 2 result partly from the fact that only new species were used). It is obvious, then, that in a large percentage of species we cannot even begin to talk about variation, potential poly-

Table 1. Pholcid spiders exemplifying our state of knowledge of one entire family. Numbers of species and proportions of the total number in various categories (columns) of known information. "1 sex" = species known from only one sex. "Many" = >20 specimens of each sex. Far right column: species for which some aspect of natural history has been studied.

Total	1 ♀ specimen	1 ♂ specimen	1 specimen	1–3 specimens	1 sex	Many specimens	Natural history
787	91 (12%)	97 (12%)	188 (24%)	313 (40%)	256 (33%)	29 (3.7%)	15 (1.9%)

Table 2. Sample of recent spider taxonomy monographs, showing respective numbers of new species described, and numbers of species in various categories (columns) of known information, e.g. "1 sex" = species known from only one sex.

References	New species	1 ♀ specimen	1 ♂ specimen	1 specimen	1–3 specimens	1 sex
Bosselaers & Jocqué (2000)	63	13	10	23	35	31
Forster & Platnick (1985)	157	30	32	62	95	80
Huber (2000, 2001)	158	0	30	30	60	50
Levi (1995, 1996, 1999)	140	31	18	49	88	93
Millidge (1991)	249	63	51	114	184	180
Platnick (2000)	171	6	8	14	53	24
TOTALS	938	143 (15%)	149 (16%)	292 (31%)	515 (55%)	458 (49%)

morphisms, and other questions relevant to the problem of species-specificity. The argument that these numbers might just be results of bad taxonomic practice is beside the point. Bad or good, they are probably representative of what the non-taxonomist will find when scanning the taxonomic literature for patterns.

The question then is, what can we conclude from that minority of species, however small, that is well studied? For example, what about those 2% of pholcid species that have been studied with respect to their biology? What about large geographic areas where higher percentages of species have been studied in some detail, like Europe or temperate North America?

The answer is not so difficult as regards the pholcids. A closer look at the literature quickly reveals that only part of the existing behavioral, morphological or distributional studies allow any conclusions relevant for the question of species-specificity of genitalia versus non-genitalia. Some of those 2% 'well-studied' species have been investigated with respect to some behavioral feature in only one population, others have been studied in more detail also morphologically, but relevant statistical and distributional data are absent. Some species (29 in Table 1) are known from large samples, and statistical data are available, allowing the assessment of, for example, polymorphism in these cases. This results in a conservative estimate of 28 pholcid species where present evidence suggests that genitalia are monomorphic and species-specific, i.e. relatively constant in shape within the species and significantly distinct from their closest relatives. With respect to polymorphism, these 28 species face one species with genitalic dimorphism (Huber & Pérez 2001a). What predictions do these numbers allow about the remaining 96% of nominal species? Not more than the vague prediction that about 3% of species will be polymorphic (i.e., 23 times as many as presently known).

The situation might seem more promising in geographic areas where many species have been studied in detail. However, to objectively quantify the number of species and species groups that have been studied with respect to the relevant questions seems impossible. For the sake of simplicity, consider only the question of genitalic polymorphism. Assume that hundreds of species have been studied in detail, in the sense that large samples have been measured, the animals have been reared, etc. How many of these studies include investigations of the genitalia (considering that these often involve time-consuming dissections)? In how many cases was the species determined initially by genitalic preparation of one or a few individuals, and then it was simply assumed that all descendants logically must have the same morphology? How many of these studies treat species (with geographic distribution) rather than local populations? How often does it happen that different morphs repre-

sent different conditional strategies and, under laboratory conditions, only one morph is produced? How often are alternative morphs treated (and neglected) as 'aberrant' individuals? How often do taxonomists find polymorphisms but misinterpret the result by postulating intermediate forms (cf. references in Hausmann 1999)? With species-specificity as a basic assumption there has been no need for studies specifically designed to prove or disprove it. Of the "hundreds of species" mentioned above, a much smaller sample would emerge with relevant data available (i.e., in our example, suggesting the absence of genitalic polymorphism). In fact, however, at least four European genera (*Euscelis* cicadas; a *Microphor* fly; *Glossotrophia* and *Scopula* moths) are known to be dimorphic with respect to the male genitalia (Müller 1957, Kunze 1959, Ulrich 1988, Hausmann 1999). As with the pholcid data set above, the sample is not nearly large enough to allow convincing generalizations, but given the fact that all cases so far were discovered by chance, it strongly stresses the need to intensify the search for genitalic polymorphisms.

Conclusions

The taxonomic evidence in favor of rapid evolution and species-specificity seems overwhelming. However, it might be worthwhile to subject these 'facts' to a rigorous quantitative analysis before accepting them as corner stones for further and far-reaching hypotheses. Where the relevant data should come from is an open question. With the present explosion of molecular techniques and data it seems reasonable to expect an answer from this field (cf. Butt et al. 1997). Molecular data provide phylogenies independent from those based on morphology, and are thus suited to test relative rates of evolution in different character systems. But taxonomists working with traditional methods also have tools to find solutions to the problems discussed: by emphasizing the fundamental biological aspect of variation in large-scale morphometric analyses; by avoiding a priori weighting of certain character systems in higher classification; and, most importantly, by keeping potential biases and constraints like those discussed above in mind, and questioning even time-honored 'rules' in their everyday work.

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References

- Alexander, R. D., Marshall, D. C. & Cooley, J. R. (1997): Evolutionary perspectives on insect mating. Pp. 4–31 in: Choe, J. C. & Crespi, B. J. (eds) *The Evolution of Mating Systems in Insects and Arachnids*. Cambridge University Press, Cambridge.
- Arnqvist, G. (1998): Comparative evidence for the evolution of genitalia by sexual selection. *Nature* 393: 784–786.
- Arnqvist, G. & Thornhill, R. (1998): Evolution of animal genitalia: patterns of phenotypic and genotypic variation and condition dependence of genital and non-genital morphology in a water strider (Heteroptera: Gerridae: Insecta). *Gen. Res.* 71: 193–212.
- Arnqvist, G., Thornhill, R. & Rowe, L. (1997): Evolution of animal genitalia: morphological correlates of fitness components in a water strider. *J. Evol. Biol.* 10: 613–640.
- Bosselaers, J. & Jocqué, R. (2000): *Hortipes*, a huge genus of tiny afrotropical spiders (Araneae, Liocranidae). *Bull. Am. Mus. Nat. Hist.* 256: 1–108.
- Butt, C. J., Blake, J. A., Adams, M. D., White, O., Sutton, G., Clayton, R., Kerlavage, A. R., Fields, C. & Venter, J. C. (1997): The impact of rapid gene discovery technology on studies of evolution and biodiversity. Pp. 289–299 in: Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O. (eds) *Biodiversity II*. Joseph Henry Press, Washington, D.C.
- Coddington, J. A. (1990): Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneocladia: Araneoidea, Deinopoidea). *Smiths. Contr. Zool.* 496: 1–52.
- Eberhard, W. G. (1985): *Sexual Selection and Animal Genitalia*. x + 244 pp., Harvard University Press, Cambridge.
- Eberhard, W. G., Huber, B. A., Rodriguez S., R. L., Briceño, R. D., Salas, I. & Rodriguez, V. (1998): One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. *Evolution* 52: 415–431.
- Erwin, T. L. (1997): Biodiversity at its utmost: tropical forest beetles. Pp. 27–40 in: Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O. (eds) *Biodiversity II*. Joseph Henry Press, Washington, D.C.
- Forster, R. R. & Platnick, N. I. (1985): A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. *Bull. Am. Mus. Nat. Hist.* 181: 1–229.
- Gavrilets, S. (2000): Rapid evolution of reproductive barriers driven by sexual conflict. *Nature* 403: 886–889.
- Hausmann, A. (1999): Falsification of an entomological rule: polymorphic genitalia in geometrid moths. *Spixiana* 22: 83–90.
- Hillis, D. M., Moritz, C. & Mable, B. K. (1996): *Molecular Systematics*. Second Edition. xvi + 655 pp., Sinauer Associates, Inc., Massachusetts.
- Hillis, D. M. & Wiens, J. J. (2000): Molecules versus morphology in systematics. Pp. 1–19 in: Wiens, J. J. (ed.) *Phylogenetic Analysis of Morphological Data*. Smithsonian Institution Press, Washington and London.
- Howard, D. J. & Berlocher, S. H. (1998): *Endless Forms, Species and Speciation*. Oxford University Press, New York.
- Hribar, L. J. (1996): Larval rearing temperature affects morphology of *Anopheles albimanus* (Diptera: Culicidae) male genitalia. *J. Am. Mosquito Contr. Assoc.* 12: 295–297.
- Huber, B. A. (2000): New World pholcid spiders (Araneae: Pholcidae): a revision at generic level. *Bull. Am. Mus. Nat. Hist.* 254: 1–348.
- Huber, B. A. (2001): The pholcids of Australia: taxonomy, biogeography, and relationships. *Bull. Am. Mus. Nat. Hist.* 260: 1–144.
- Huber, B. A. & Pérez González, A. (2001a): A new genus of pholcid spiders (Araneae: Pholcidae) endemic to western Cuba, with a case of female genitalic dimorphism. *Am. Mus. Novitates* 3329: 1–23.
- Huber, B. A. & Pérez González, A. (2001b): Female genitalic dimorphism in a spider (Araneae: Pholcidae). *J. Zool. (London)* 255: 301–304.
- Inger, R. F. & Marx, H. (1962): Variation of hemipenis and cloaca in the colubrid snake *Calamaria lumbricoidea*. *Syst. Zool.* 11: 32–38.
- Jocqué, R. (1998): Female choice, secondary effect of “mate check”? A hypothesis. *Belg. J. Zool.* 128: 99–117.
- Kitching, I. J., Forey, P. L., Humphries, C. J. & Williams, D. M. (1998): *Cladistics*. Second Edition. xiii + 228 pp., Oxford University Press, Oxford.
- Kunze, L. (1959): Die funktionsanatomischen Grundlagen der Kopulation der Zwergzikaden, untersucht an *Euscelis plebejus* (Fall.) und einigen Typhlocybinen. *D. Entomol. Z. (NF)* 6: 322–387.
- Levi, H. W. (1995): The neotropical orb-weaver genus *Metazygia* (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* 154: 63–151.
- Levi, H. W. (1996): The American orb-weavers *Hypognatha*, *Encycosaccus*, *Xylethrus*, *Gasteracantha* and *Enacrosoma* (Araneae, Araneidae). *Bull. Mus. Comp. Zool.* 155: 1–157.
- Levi, H. W. (1999): The neotropical and Mexican orb weavers of the genera *Cyclosa* and *Allopecosa* (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* 155: 299–379.
- Mayr, E. (1955): Karl Jordan’s contributions to current concepts in systematics and evolution. *Trans. R. Entomol. Soc. Lond.* 107: 45–66.
- Mayr, E. & Ashlock, P. D. (1991): *Principles of Systematic Zoology*. Second Edition. xx + 475 pp., McGraw-Hill, Inc., New York.
- Millidge, A. F. (1991): Further linyphiid spiders (Araneae) from South America. *Bull. Am. Mus. Nat. Hist.* 205: 1–199.
- Mound, L. A., Crespi, B. J. & Tucker, A. (1998): Polymorphism and kleptoparasitism in thrips (Thysanoptera: Phlaeothripidae) from woody galls on *Casuarina* trees. *Austr. J. Entomol.* 37: 8–16.
- Müller, H. J. (1957): Die Wirkung exogener Faktoren auf die zyklische Formenbildung der Insekten, insbesondere der Gattung *Euscelis* (Hom. Auchenorrhyncha). *Zool. Jb., Abt. Syst. Oekol. Geogr. Tiere* 85: 317–430.
- Pierre, J. (1992): Systématique évolutive et cladistique: approche morphologique, spéciation et génation, application chez les *Acraea* (Lepidoptera, Nymphalidae). *Bull. Soc. Entomol. France* 97: 105–118.
- Platnick, N. I. (1975): A revision of the palimanid spiders of the new subfamily Otiothopinae (Araneae, Palpimanidae). *Am. Mus. Novitates* 2562: 1–32.

- Platnick, N. I. (2000): A relimitation and revision of the Australasian ground spider family Lamponidae (Araneae: Gnaphosoidea). *Bull. Am. Mus. Nat. Hist.* 245: 1–330.
- Stevens, P. F. (1991): Character states, morphological variation, and phylogenetic analysis: a review. *Syst. Bot.* 16: 553–583.
- Stork, N. E. (1993): How many species are there? *Biodiv. Conserv.* 2: 215–232.
- Stork, N. E. (1997): Measuring global diversity at its decline. Pp. 41–68 in: Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O. (eds) *Biodiversity II*. Joseph Henry Press, Washington, D.C.
- Thom, R. (1996): Qualitative and quantitative in evolutionary theory with some thoughts on Aristotelian Biology. *Mem. Soc. Ital. Sci. Nat. Mus. Civ. Sto. Nat., Milano* 27: 115–117.
- Ulrich, H. (1988): Das Hypopygium von *Microphor holosericeus* (Meigen) (Diptera, Empidoidea). *Bonn. Zool. Beitr.* 39: 179–219.
- Vitalievna, N. M. (1995): Seasonal variation in the male genitalia of *Plagodis dolabraria* (Linnaeus, 1758) (Lepidoptera, Geometridae). *Atalanta* 26: 311–313.