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Sexual selection according to Darwin: A response to Padian and Horner's interpretation

La sélection sexuelle selon Darwin : une réponse à l'interprétation de Padian et Horner

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ABSTRACT

The interpretation of exaggerated structures in the vertebrate fossil record has been hampered by disagreement over the definition of sexual selection and how it relates to sexual dimorphism. Previous assertions that Darwin placed a requirement of sexual dimorphism on sexual selection are mistaken. Instead, Darwin describes variation within one sex and the exertion of a struggle (expressed as intrasexual competition, intersexual mate choice, or both) as the necessary components of sexual selection. The use of structures by one sex to attract mates or repel rivals for mates occurs independently of any existing sexual differences. Differential mating success is also a requirement of Darwinian sexual selection. Mutual sexual selection is a legitimate concept that was described by Darwin. Sexual selection remains a viable explanatory hypothesis for the presence of exaggerated structures of extinct organisms and need not be dismissed summarily, but should not be employed without support as a default hypothesis.

Mots clés :
Sélection sexuelle
Dimorphisme sexuel
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RÉSUMÉ

L'interprétation de structures exagérées observées chez de nombreux vertébrés fossiles a été entravée par un désaccord sur la définition de la sélection sexuelle et sur son lien avec le dimorphisme sexuel. De précédentes publications rapportant que Darwin avait affirmé que la présence d'un dimorphisme sexuel était nécessaire pour la sélection sexuelle sont dans l'erreur. En réalité, Darwin a établi que la présence de variation au sein des membres d'un sexe et l'existence d'une lutte (exprimée en termes de sélection intrasexuelle, sélection intersexuelle, ou les deux) sont les composantes nécessaires de la sélection sexuelle. L'utilisation de structures par les membres d'un sexe pour attirer des partenaires sexuels ou afin de repousser des rivaux se produit indépendamment de la présence de différences sexuelles. Pour que les effets de la sélection sexuelle darwinienne soient perceptibles, un taux différentiel du succès reproductif doit être présent.

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La sélection sexuelle mutuelle est un concept légitime qui a été décrit par Darwin. En conséquence, la sélection sexuelle demeure une hypothèse valable pour expliquer la présence de structures exagérées chez les organismes disparus et ne doit pas être rejetée sommairement, bien qu'elle nécessite de s'appuyer sur des éléments de preuve.

1. Introduction

There is an ongoing debate in the palaeontological literature concerning 'bizarre' or exaggerated structures and their relationship to sexual selection, sexual dimorphism, and species recognition. This debate was sparked by arguments raised by Padian and Horner (2011a) and includes responses, opinions, and reviews by Knell and Sampson (2011), Dodson (2011), Padian and Horner (2011b), Hone et al. (2012), Knell et al. (2013a), Padian and Horner (2013), Knell et al. (2013b), Hone and Naish (2013), Mendelson and Shaw (2012, 2013), and most recently, Padian and Horner (2014).

An important component of this discussion is the definition of 'sexual selection' advanced by Padian and Horner (2011a, 2011b, 2013, 2014). These authors very clearly state what they consider to be Darwin's definition of sexual selection (Padian and Horner, 2011a, 2011b, 2013, 2014) and explicitly address its implications for palaeontology. However, other authors have raised concerns with this definition. Knell and Sampson (2011) disagreed (as did Taylor et al., 2011) with the necessary correlation between strict sexual dimorphism and sexual selection that Padian and Horner (2011a) endorse, but they did not pursue those concerns to their roots. These concerns were addressed more directly by Knell et al. (2013b), who criticized the restrictive nature of Padian and Horner's definition as well as their interpretation of Darwin's description of sexual selection. Despite these rebuttals, the issue persists (Padian and Horner, 2014). As a result, we feel that Padian and Horner's (2011a, 2011b, 2013, 2014) conceptualization of Darwinian sexual selection merits a more thorough review than it has received to date in order to clarify the terminology involved and to allow the discussion about exaggerated structures to move forward.

What we argue here is less a matter of interpretation, and more a matter of reference. We attempt to illustrate, through Darwin's own words, that Padian and Horner's (2011a, 2011b, 2013, 2014) statements about the concept of Darwinian sexual selection are not appropriately representative. We begin by addressing the related and implicated topic of sexual dimorphism.

2. Sexual dimorphism

As shown in the following examples, Padian and Horner (2011b, 2013, 2014) repeatedly assert that sexual dimorphism is integral to the concept of sexual selection. They make it very clear that by 'dimorphism' they are referring to discrete structures that are present *in one sex and not in the other*, and not simply to allometric differences between the sexes or differences in absolute size (such as sexual size dimorphism [SSD]). Furthermore, they advocate that this is also what Darwin meant:

> "Darwin cannot be 'wrong' about the definition of this concept [sexual selection], despite the protests or confusion of later authors, because he invented it, and his empirical basis for it is entirely valid; he was not 'imprecise' (*pace* Carranza, 2009). Myriad examples prove the presence of distinct, monosexual characters in species that are used to attract mates and repel rivals (Andersson, 1994; Darwin, 1871). Thus, the only possible definition of sexual selection requires sexual dimorphism (and not simply allometric sexual differences: Padian & Horner, 2010)." (Padian and Horner, 2011b:1).
>
> "But these revisionary definitions are misguided: there can be no concept of sexual selection without sexual dimorphism (and not just allometric size difference, as between males and females of many species)." (Padian and Horner, 2011b:2).
>
> "Sexual selection was invented precisely to explain unusual dimorphic structures used in mating and, therefore, dimorphism is essential to it." (Padian and Horner, 2013:1).
>
> "Sexual selection requires critical differences between males and females, and "mutual sexual selection" entails the two sexes selecting the same feature in the other sex, which is distinctly different from Darwin's definition, where the critical feature differs between the sexes." (Padian and Horner, 2014:6).
>
> "One sex must possess a feature that the other lacks (or does not use), and it is used to repel rivals or attract mates. Sexual selection therefore requires dimorphism." (Padian and Horner, 2014:10).

Padian and Horner insist on a strict definition of 'dimorphism' (but also appear to include behaviours and 'not using a feature' within the concept of morphology–we are unsure how these can be examples of dimorphism and, more particularly, how these could be applied to the fossil record). Regardless, the interpretation that sexual dimorphism is the core of sexual selection is problematic. Briefly stated, our concerns centre upon the following: (1) Darwin never used the term sexual dimorphism to describe differences between the sexes; (2) Darwin describes allometric sexual differences as products of sexual selection, and presents sexual monomorphism as an acceptable outcome of sexual selection; (3) Darwin states that sexual selection depends on variation within a sex, and that this variation is independent of the action of selection; (4) Darwin identifies his own bias for discussing

structures that would be recognised today as being sexually dimorphic. We address each of these points in turn, providing examples from Darwin's writing to support our case.

(1) Darwin never used the term 'sexual dimorphism' to describe differences between the sexes. In *The Descent of Man* (1st and 2nd eds.), Darwin (1871, 1874) never uses the term 'sexual dimorphism'. This is not surprising, nor is it a valid argument on its own, because 'sexual dimorphism' was not coined at the time, and only entered the biological literature in 1888 (Rolleston and Jackson, 1888:238) (the first tentative usage of 'dimorphism' in reference to differences between sexes is also by Rolleston [1870:cxi]). However, it does make arguing about Darwin's definition of sexual dimorphism a moot point, and raises the question as to what Padian and Horner's statements are based upon. More importantly, it gives us reason to assess the nature of the sexual differences that Darwin does describe. As shown above, Padian and Horner (2011b, 2013, 2014) insist that those differences are discretely dimorphic, with no intermediate gradations and without consideration of allometry or body size. This is in stark contrast to what Darwin actually described, as illustrated in the following section. (We further discuss Darwin's use of the term 'dimorphic' in a subsequent section.)

(2) Darwin describes allometric sexual differences as products of sexual selection, and presents sexual monomorphism as an acceptable outcome of sexual selection:

Here we come to one of the major concerns with Padian and Horner's interpretation. Their requirement of sexual dimorphism has been criticised previously (Knell and Sampson, 2011; Knell et al., 2013b), and we herein extend this critique. If strict sexual dimorphism is necessary for sexual selection (the action or invocation thereof), any number of examples from Darwin could support Padian and Horner's case, but even one contrary example could reject it. Darwin (1874) provides several such contrary examples:

> "If the males had been habitual fighters, *the size of their bodies would probably have been increased through sexual selection*, so as to have exceeded that of the female;. . ." (Darwin, 1874:297; emphasis our own).
> "As in many kinds of fishes the males habitually fight together, it is surprising that they have not generally become *larger and stronger than the females through the effects of sexual selection*. . . .Increased size must be in some manner of more importance to the females, than strength and size are to the males for fighting with other males; and this perhaps is to allow of the production of a vast number of ova." (Darwin, 1874:335; emphasis our own).
> "The males of many birds are larger than the females, and this no doubt is the result of the advantage gained by the larger and stronger males over their rivals during many generations. . . .In some few cases, as we shall hereafter see, the females apparently have acquired their greater size and strength for the sake of conquering other females and obtaining possession of the males." (Darwin, 1874:362).
> "We shall hereafter see that many animals exist, of which neither sex is brilliantly coloured or provided with special ornaments, *and yet the members of both sexes or of one alone have probably acquired simple colours, such as white or black, through sexual selection*." (Darwin, 1874:226; emphasis our own).
> "The laws of inheritance determine whether characters gained through sexual selection by either sex shall be transmitted to the same sex, or to both; as well as the age at which they shall be developed. . . .Hence secondary sexual characters, when equally transmitted to both sexes can be distinguished from ordinary specific characters only by the light of analogy." (Darwin, 1874:614).

That sexual selection can contribute to the evolution of allometric size differences, SSD, monomorphism, or gradients in morphology between the sexes, is clearly expressed by Darwin and is an essential component of the theory.

(3) Darwin states that sexual selection depends on variation within a sex, and that this variation is independent of the action of selection:

Sexual dimorphism does not relate to the process of sexual selection. According to Darwin, the competition only ever occurs between members of a single sex and has nothing to do with the relative features of the opposite sex, even in instances of mate choice or mutual sexual selection. The requirement is for morphological variation within one sex and for a 'struggle' to exert a selection pressure upon that variation.

> "Sexual selection depends on the success of certain individuals *over others of the same sex*, in relation to the propagation of the species. . . The sexual struggle is of two kinds; in the one it is between individuals of the same sex, generally the males, in order to drive away or kill their rivals, the females remaining passive; whilst in the other, the struggle is likewise between the individuals of the same sex, in order to excite or charm those of the opposite sex. . ." (Darwin, 1874:614; emphasis our own)
> "A slight degree of variability leading to some advantage, however slight, in reiterated deadly contests would suffice for the work of sexual selection; and it is certain that secondary sexual characters are eminently variable." (Darwin, 1874:211)
> "As sexual selection primarily depends on variability, a few words must be added on this subject." (Darwin, 1874:319)
> "Variability is the necessary basis for the action of selection, and is wholly independent of it." (Darwin, 1874:615)

There is no requirement for sexual dimorphism or monosexual characters. Mate competition and mate choice are essential components of sexual selection.

(4) Darwin identifies his own bias for addressing structures that would be recognised today as being sexually dimorphic:

Padian and Horner repeatedly assert that because Darwin describes numerous sexually dimorphic structures, those structures therefore define sexual selection. This logic is flawed: the demonstrable outcomes of selection

do not define its inner workings, they merely illustrate them. Darwin (1874) focussed on obviously differing structures in order to clearly illustrate his theory and to address some of the most contentious structures (several of which, although certainly not all, are indeed dimorphic in the discrete, monosexual sense described by Padian and Horner), but he stated this preference and bias directly.

> "So again, if the chief service rendered to the male by his prehensile organs is to prevent the escape of the female before the arrival of other males, or when assaulted by them, these organs will have been perfected through sexual selection, that is by the advantage acquired by certain individuals over their rivals. *But in most cases of this kind it is impossible to distinguish between the effects of natural and sexual selection*. Whole chapters could be filled with details on the differences between the sexes in their sensory, locomotive, and prehensile organs. *As, however, these structures are not more interesting than others adapted for the ordinary purposes of life, I shall pass them over almost entirely, giving only a few instances under each class*." (Darwin, 1874:210; emphasis our own)

Darwin states that whole chapters could be filled with the details of mundane sexual differences attributable to sexual selection, but that he is going to skip to the most interesting examples. In *The Descent of Man*, Darwin (1874) described the process by which such interesting forms could arise, so he chose the most prominent examples to illustrate his points. Nowhere in the text, though, does he suggest that sexual selection requires, or can only operate on, pre-existing monosexual structures or characters. It appears that Padian and Horner (2011a, 2011b, 2013, 2014) have inverted this by focusing on Darwin's (1874) examples of some eye-catching products of sexual selection while ignoring the process, the very concept that Darwin was trying to elucidate.

2.1. Defining dimorphism

As previously mentioned, there has been some confusion surrounding Darwin's use of the term 'dimorphism'.

> "Dimorphism is not simply difference; size difference is not dimorphism in Darwin's sense because it does not describe a structure, function, or behavior that one sex has and the other does not." (Padian and Horner, 2014:10)

This attribution is inaccurate. As mentioned, Darwin does not use the term 'sexual dimorphism' in *The Descent of Man* (1871, 1874). However, he does use the term 'dimorphism' (or 'dimorphic') several times and was the first to use the term in a biological context (in the fourth edition of *The Origin of Species* [1866]. Previous usage was restricted to crystallography [OED Online, 2013]). In all instances, it is very clear that Darwin is referring to two distinct forms of a structure, or colours, within a single sex, with an absence of intermediate forms or gradations between them. His meaning is best illustrated by his description of the beetle *Siagonium* on page 299 (1874), and in the footnote on that page, as well as by his description of the dimorphic elytra of female water beetles, in footnote 6 on page 276 (1874).

From these examples, and others in *The Descent of Man* (1874; see p. 265, 268, 273, 291, and 484), it is clear that Darwin used the term in strict accord with its traditional meaning ("of two forms" [OED Online, 2013]) to describe the presence of distinct morphologies or morphological traits, without intermediate gradations, and only ever within a single sex. He was clearly using the term judiciously. It is worth reiterating, then, that Darwin (1874) never once used the term 'dimorphic' to explain the differences that he was describing between the sexes, only within them. But when it came to sexual selection, Darwin described sexual differences of all kinds, including differences in body size and allometric growth.

3. Sexual selection

Padian and Horner (2013) assert that sexual selection *sensu* Darwin has three components:

> "Because Darwin invented sexual selection, and based it on copious observations [2] that have never been falsified, his definition cannot be wrong. It has three components: (i) it explains why sexual dimorphism exists, and its central role in sexual selection; (ii) the dimorphic structures or behaviors are used by one gender to attract mates or repel rivals for mates; and (iii) these structures and behaviors help the bearer gain access to mates (not necessarily to leave more offspring, but to leave offspring that are more competitive in mating)." (Padian and Horner, 2013:1). (Note that this definition is repeated verbatim in Padian [2013] and the following critique applies to both instances.)

Despite the insistence by Padian and Horner that they are deferring to Darwin, and therefore cannot be wrong (see comments by Knell et al. [2013b] regarding the descent with modification of scientific theories), a close reading of what Darwin actually wrote raises concerns with their definition. There are problems with all three components, each of which we address in turn:

(i) "It explains why sexual dimorphism exists, and its central role in sexual selection;" (Padian and Horner, 2013:1).

Sexual selection theory does explain, in large part, why sexual dimorphism exists, and it was observations of sexual dimorphism that spurred Darwin to explore the concept in the first place. Despite this, it is well known now that there are other paths by which sexual dimorphism may arise within a lineage, and it is important to note that Darwin was aware of this as well, providing in *The Descent of Man* a list of examples of sexual dimorphisms that he suggests are not attributable to the process of sexual selection (Darwin, 1874:208). More importantly, the second clause "[sexual dimorphism's] central role in sexual selection" is simply not so, as was discussed above.

(ii) "The dimorphic structures or behaviors are used by one gender to attract mates or repel rivals for mates;" (Padian and Horner, 2013:1):

As mentioned, there is no requirement of sexually dimorphic structures for sexual selection to occur, only for variation *within* a sex (and for "the ardour in love, the courage, and the rivalry of the males, as well as . . . the powers of perception, the taste, and will of the female." [Darwin, 1874:240]). That structures or behaviours are used by one gender to attract mates or repel rivals for mates occurs *independently* of any existing sexual differences. This point is crucial to the entire concept of sexual selection and is made repeatedly by Darwin:

> "We are, however, here concerned only with sexual selection. This depends on the advantage which certain individuals have over others *of the same sex* and species solely in respect of reproduction." (Darwin, 1874:209; emphasis our own.)
> "This does not depend on any superiority in the general struggle for life, *but on certain individuals of one sex*, generally the male, being successful in conquering other males, and leaving a larger number of offspring to inherit their superiority than do the less successful males." (Darwin, 1874:553; emphasis our own.)
> "Sexual selection depends on the success *of certain individuals over others of the same sex*, in relation to the propagation of the species;. . ." (Darwin, 1874:614; emphasis our own).

(iii) "These structures and behaviors help the bearer gain access to mates (not necessarily to leave more offspring, but to leave offspring that are more competitive in mating)." (Padian and Horner, 2013:1):

Padian and Horner (2013) are correct in stating that Darwinian sexual selection is not simply about leaving more offspring and that it cannot be invoked by a reduction to numerical 'fitness'. However, for Darwinian sexual selection to operate as an evolutionary process, differential mating success within the sexes is required (i.e. eventually someone *does* have to leave more offspring than their rivals). Darwin identifies this requirement of sexual selection numerous times:

> "Our difficulty in regard to sexual selection lies in understanding how it is that the males which conquer other males, or those which prove the most attractive to the females, leave a greater number of offspring to inherit their superiority than their beaten and less attractive rivals. *Unless this result does follow, the characters which give to certain males an advantage over others, could not be perfected and augmented through sexual selection.*" (Darwin, 1874:213; emphasis our own).
> "But in other cases the males during long ages may have struggled together for the possession of the females, and yet no effect will have been produced, unless a larger number of offspring were left by the more successful males to inherit their superiority, than by the less successful: and this, as previously shewn [sic], depends on many complex contingencies." (Darwin, 1874:226).
> "I have not attempted to conceal that, excepting when the males are more numerous than the females, or when polygamy prevails, it is doubtful how the more attractive males succeed in leaving a larger number of offspring to inherit their superiority in ornaments or other charms than the less attractive males; but I have shewn [sic] that this would probably follow from the females,–especially the more vigorous ones which would be the first to breed,– preferring not only the more attractive but at the same time the more vigorous and victorious males." (Darwin, 1874:615).

See also the quotation provided in (ii) above, from (Darwin, 1874:614).

So, all three components of Padian and Horner's (2013) definition of Darwinian sexual selection are inconsistent with Darwin's own statements.

3.1. Mutual sexual selection

Padian and Horner (2014:6) state that: "As for "mutual sexual selection," Darwin never used the term (*contra* Jones and Hunter, 1993, and others)." This is an unsupported statement given that Darwin wrote:

> "There are, however, many animals in which the sexes resemble each other, both being furnished with the same ornaments, which analogy would lead us to attribute to the agency of sexual selection. In such cases it may be suggested with more plausibility, that there has been a double or mutual process of sexual selection; the more vigorous and precocious females selecting the more attractive and vigorous males, the latter rejecting all except the more attractive females." (1874:225).

Darwin clearly did use the term, as was previously shown by Knell et al. (2013b), and he coined the concept. Furthermore, Darwin goes on to say, "But from what we know of the habits of animals, this view is hardly probable, for the male is generally eager to pair with any female," (1874:225). Does he reject the concept of mutual sexual selection on theoretical grounds? No. Rather, Darwin says it is an unlikely explanation given what was known at the time, effectively inviting future generations of biologists to seek evidence of discrimination in male mate choice, which would lend support to his idea of mutual sexual selection. Finally, as for the statement that mutual sexual selection is an oxymoron because it violates Darwin's requirement for sexual dimorphism (Padian and Horner, 2014:6), that logic has already been refuted.

3.2. The hierarchy of concepts in sexual selection

Padian and Horner assert that "If one does not accept that dimorphism is required for sexual selection (regardless of Darwin's exhaustive documentation), it becomes difficult to separate Darwin's original concept of sexual selection from other related ideas with which it is frequently conflated." (2014:6). Not accepting their requirement for sexual dimorphism does make it difficult to accept the separation of concepts that they present, because that hierarchy is also incongruent with Darwin's writing. As was shown previously, mate competition and mate choice are fundamental components of Darwin's conceptualization of sexual selection: the action of either, when enforced through differing reproductive success,

forms the selection component of sexual selection. These cannot be teased apart, contrary to the assertions of Padian and Horner (2014), without distorting Darwin's concept of sexual selection. This holds true for modern conceptualizations as well: mate choice and mate competition remain the core agents of sexual selection and are still being actively studied in that context (see Miller and Svensson, 2014). If a Hierarchy of Concepts is to be advanced, mate choice and mate competition should be on par with one another as components of sexual selection, not precedents to it.

4. Moving forward

As stated by Arnold (1994:2), "A definition of sexual selection matters because it affects the conduct of science." We have shown here that Padian and Horner's *ipse dixit* statement that sexual selection requires sexual dimorphism because Darwin said so, is not supported. Rectifying the misconceptions surrounding sexual selection creates a more constructive space in which the 'bizarre' structures of dinosaurs and other extinct animals (as well as the processes by which they arose, were maintained, or were modified) can be investigated. For example, Padian and Horner (2014:5) stated that they have shown that "[Darwinian sexual selection's] application to extinct dinosaurs and their relatives is unsubstantiated," based on "the absence of any evidence that these taxa showed Darwin's requirement of sexual dimorphism." Rejecting this false requirement reopens the door to testing the legitimate hypothesis that sexual selection influenced the evolutionary history of these taxa (e.g. mutual sexual selection of ornithodiran head crests [Hone et al., 2012]).

We agree with Padian and Horner (2014), among others (Hone et al., 2012; Knell et al., 2013a), that sexual selection should not be viewed as a default hypothesis for 'bizarre' structures, and that it must be tested and supported by evidence. Unfortunately, there is no silver bullet test for sexual selection in the fossil record—but the development of a structure or character in a late ontogenetic stage, the heightened variability of a particular structure within a population, or the demonstration of a bimodal distribution (or of dimorphism) within an adult population, would all provide some measure of support for the hypothesis that sexual selection played a role in the evolutionary history of that taxon. Of course, none of those tests apply only to sexual selection, nor would their rejection definitively rule it out (such as an absence of dimorphism). These are not new ideas; they have been previously discussed by Knell et al. (2013a) and Hone and Naish (2012), and are only being repeated here because they can be readily drawn from Darwin's (1874) writing on sexual selection.

With mate choice and mate competition repositioned as components of sexual selection, they become 'prerequisites' only in the sense that one, or both, should be considered before proposing sexual selection as an explanatory hypothesis for features in the fossil record; support for either is, by definition, support for sexual selection. This may provide a simple criterion of sorts to curb 'default' acceptance of sexual selection: without support for mate choice or mate competition there is likely not support for sexual selection.

We believe that the study of sexual selection in vertebrate palaeontology is becoming more interesting now than it has ever been. But without a shared understanding of the terminology involved, the field will not be able to advance. We hope that the interpretation of Darwin's (1871, 1874) writings that we have presented has clarified some of the confusion surrounding sexual selection and will allow this area of study to move forward.

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References

Andersson, M., 1994. Sexual selection. Princeton University Press, Princeton (599 p.).
Arnold, S.J., 1994. Is there a unifying concept of sexual selection that applies to both plants and animals? Amer. Nat. 144 (Suppl.), S1–S12.
Carranza, J., 2009. Defining sexual selection as sex dependent selection. Anim. Behav. 77, 749–751.
Darwin, C., 1866. On the origin of species by means of natural selection, 4th ed. John Murray, London (593 p.).
Darwin, C., 1871. The descent of man and selection in relation to sex. John Murray, London (828 p.).
Darwin, C., 1874. The descent of man and selection in relation to sex, 2nd ed. John Murray, London (688 p.).
Dodson, P., 2011. Sex in the Cretaceous–How to tell the girls from the boys. Am. Paleontol. 19 (3), 21–24.
Hone, D.W.E., Naish, D., 2013. The 'species recognition hypothesis' does not explain the presence and evolution of exaggerated structures in non-avialan dinosaurs. J. Zool. 290, 172–180.
Hone, D.W.E., Naish, D., Cuthill, I.C., 2012. Does mutual sexual selection explain the evolution of head crests in pterosaurs and dinosaurs? Lethaia 45, 139–156.
Jones, J.L., Hunter, F.M., 1993. Mutual sexual selection in a monogamus seabird. Nature 362, 238–239.
Knell, R.J., Sampson, S., 2011. Bizarre structures in dinosaurs: species recognition or sexual selection? A response to Padian and Horner. J. Zool. 283, 18–22.
Knell, R.J., Naish, D., Tomkins, J.L., Hone, D.W.E., 2013a. Sexual selection in prehistoric animals: detection and implications. Trends Ecol. Evol. 28, 38–47.
Knell, R.J., Naish, D., Tomkins, J.L., Hone, D.W.E., 2013b. Is sexual selection defined by dimorphism alone? A reply to Padian and Horner. Trends Ecol. Evol. 28, 250–251.
Mendelson, T.C., Shaw, K.L., 2012. The (mis)concept of species recognition. Trends Ecol. Evol. 27, 421–427.
Mendelson, T.C., Shaw, K.L., 2013. Further misconceptions about species recognition: a reply to Padian and Horner. Trends Ecol. Evol. 28, 252–253.
Miller, C.W., Svensson, E.I., 2014. Sexual selection in complex environments. Annu. Rev. Entomol. 59, 427–445.
OED, 2013. Online "dimorphism, n.". Oxford University Press http://www.oed.com/view/Entry/52947
Padian, K., 2013. Correcting some common misrepresentations of evolution in textbooks and the media. Evol. Educ. Outreach. 6 (1), 11.
Padian, K., Horner, J.R., 2011a. The evolution of 'bizarre structures' in dinosaurs: biomechanics, sexual selection, social selection or species recognition? J. Zool. 283, 3–17.
Padian, K., Horner, J.R., 2011b. The definition of sexual selection and its implications for dinosaurian biology. J. Zool. 283, 23–27.
Padian, K., Horner, J.R., 2013. Misconceptions of sexual selection and species recognition: a response to Knell et al. and to Mendelson and Shaw. Trends Ecol. Evol. 28, 249–250.

Padian, K., Horner, J.R., 2014. The species recognition hypothesis explains exaggerated structures in non-avialan dinosaurs better than sexual selection does. C. R. Palevol 13, 97–107.
Rolleston, G., 1870. Forms of animal life. Oxford University Press, Oxford (237 p.).
Rolleston, G., Jackson, W.H., 1888. Forms of animal life, 2nd ed. Oxford University Press, Oxford (937 p.).
Taylor, M.P., Hone, D.W.E., Wedel, M.J., Naish, D., 2011. The longs necks of sauropods did not evolve through sexual selection. J. Zool. 285, 150–161.