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The species recognition hypothesis explains exaggerated structures in non-avian dinosaurs better than sexual selection does



L'hypothèse de la reconnaissance de l'espèce explique mieux que la sélection naturelle des structures exagérées chez les dinosaures non aviens

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ABSTRACT

Several hypotheses have been proposed to explain “bizarre structures” in dinosaurs and other extinct animals (e.g., mechanical function and several kinds of intra- and interspecific display). Recent evidence and tests for species recognition as a possible driver of these structures have been proposed, in particular as an alternative to traditional hypotheses of function and sexual selection, which have fallen short. Advocates of sexual selection and mechanical function have advanced untested hypotheses claiming that species recognition cannot be an important process in evolution. We address these claims and show that they are based on misreading of the evidence and of previous literature. We also acknowledge that there have been historically differing definitions of sexual selection, which have greatly impeded understanding of the whole phenomenon of mate attraction and choice. Particularly in fossil animals, it is impossible to accept any hypothesis as the “default” that does not require evidence or testing to establish it.

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R É S U M É

Certaines hypothèses ont été proposées pour expliquer des « structures bizarres » chez les dinosaures ou chez d'autres animaux disparus (par exemple fonction mécanique, différentes sortes d'affichage intra- et interspécifique). Des preuves et tests récents pour une reconnaissance de l'espèce en tant que facteur déterminant de ces structures ont été proposés, en particulier comme alternative aux hypothèses traditionnelles de sélection sexuelle et de fonction, mais ont été un échec. Les avocats de la sélection sexuelle et de la fonction mécanique ont avancé des hypothèses non testées, affirmant que la reconnaissance de l'espèce ne peut constituer un processus important au cours de l'évolution. Nous présentons ces affirmations et montrons qu'elles sont fondées sur une lecture erronée des preuves et de la littérature antérieure. Nous admettons aussi qu'il y a eu historiquement différentes définitions de la sélection sexuelle, qui ont gêné la compréhension du phénomène

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d'attraction et de choix du partenaire dans son ensemble. En particulier, chez les animaux fossiles, il est impossible d'accepter quelque hypothèse que ce soit de défaut (ou de manque) qui ne requière de preuve ou de test pour l'établir.

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1. Introduction

Several mechanisms have been historically advanced to explain variations in the bizarre skeletal structures of dinosaurs such as horns, frills, plates, spikes, crests, and domes (Main et al., 2005; Padian and Horner, 2011a, 2011b), including mechanical functions and several kinds of display (intraspecific and interspecific, including species recognition, mate recognition, social selection, and sexual selection). The considerable difference of opinion on the relative importance of such mechanisms and how to recognize them proceeds from two main sources. First, different workers use different definitions, some strongly altered from their original meanings. Second, no mechanisms can be assumed to have been prevalent in extinct animals based on weak analogy to living animals; there must be specific and diagnostic comparisons. However difficult it is to understand the behavior of living animals, it is much harder to understand what behaviors were associated with structural changes in extinct ones. “Default” hypotheses for these structures cannot be accepted merely on vague comparisons to selected living examples.

Our position is that Darwin defined sexual selection for a specific reason and that it requires specific criteria, but these criteria have been lost as the recent generation of biologists has neglected to read his work and has instead reduced his concept to a vague formulation of mating advantage, however it is acquired. In so doing the concepts of mate recognition, mate choice, and mate competition have been frequently confused with and even equated with sexual selection. We show that there is considerable value in differentiating among these concepts and respecting Darwin's original formulation. In turn, we think that the concept of species recognition is far more important than usually recognized, has been traditionally neglected by biologists, and is testable, either by itself or in concert with other processes, as a promoter of species differentiation. This does not mean that it explains everything or most things, but it should not be dismissed. There is now a considerable sample of fossil material available for testing in its morphological, stratigraphic, ecological, and geographic contexts.

In a recent paper, Hone and Naish (2013) make several statements about the interpretation of exaggerated or “bizarre” structures (Padian and Horner, 2011a, 2011b) in non-avian dinosaurs that are incorrect. They claim that species recognition could not have been important in extinct animals because (according to them) it is not observed, or not important, in living animals. They recur to discredited arguments about sexual selection in non-avian dinosaurs, even though every case purported to demonstrate sexual selection in these dinosaurs (and other Mesozoic archosaurs) has been rejected or shown to have

no evidentiary basis. In contrast, species recognition, as we define it (and there are several definitions in the literature), is probably more important than heretofore recognized in both living and extinct animals, and it likely worked in concert with other processes to promote species diversity and morphological evolution.

Here we evaluate the claims of various authors about sexual selection and species recognition as they relate to extinct animals, and we reset the concepts of species recognition, sexual selection, and related terms in a logical hierarchical scheme.

2. Claim 1. Only processes that have been observed in available living animals (i.e., those animals that have been adequately studied to date) were present in extinct animals

For example, Hone and Naish (2013) claim that “multi-functionality for many such [bizarre] structures is probable, given extant analogues”; however, “invoking species recognition as the primary selective mechanism driving the evolution of such structures is problematic given the lack of evidence for this in extant species”; that “fossil animals must have been subject to the same selection pressures as extant ones” (how can one know “selection pressures” in extinct animals?); and that “non-avian dinosaurs were likely similar to extant animals and probably used multiple signals as identifiers” (our emphases).

These arguments violate the concept of *uniformitarianism*, the philosophical foundation of science. True uniformitarianism holds only that the *laws of nature* are immanent, and by no means can one assume that the processes and patterns that governed extinct creatures and their environments are restricted by what is available to observe in the present day. So it is incorrect to claim that because we have not yet observed (or looked for, or intensively studied) a process in today's world, the process could not have existed in the past or was not important.

Moreover, arguments cannot be justified solely on the basis of analogies, because they do not provide evidence for anything, and are merely rhetorical devices. To substantiate analogies, *specific* structures between analogized groups must be identical in order to postulate similar functions. For example, dinosaur cranial ornamentations are vastly different than they are in dimorphic birds and mammals. On the other hand, Darwin's (1859) classic analogy between artificial and natural selection works because he was able to show that both processes depend upon natural, inherited variations that succeed differentially under given circumstances; in fact, his comparison was ultimately based on the homology of genetics.

3. Claim 2. There is no evidence for species recognition in living animals—or, at least, that species recognition is important in shaping traits

For example, Hone and Naish (2013) state that “there has yet to be any documented case in *any extant species* where a crest or similar structure functions primarily in species recognition” (and therefore this was impossible in extinct taxa); “[t]hat *no extant species*, including the thousands of *extant dinosaurs* [i.e., birds], has yet been demonstrated to use exaggerated morphological structures for the purposes of ‘species recognition’ argues against the idea that we should assume such a role among Mesozoic taxa”; “[g]iven that *extant taxa* do not appear to be using these [bizarre] structures for species recognition, a plausible mechanism is required to explain their origin, retention and propagation, and to our knowledge none has been proposed”; and that “[t]here is currently no evidence that *in extant taxa*, exaggerated structures have evolved primarily through species recognition” (again, our emphases).

In trying to minimize the possible importance of species recognition, Hone and Naish misrepresent the work of Harrison and Poe (2012), who they say “specifically tested the species recognition hypothesis with respect to the presence of exaggerated structures and found it wanting.” In fact, Harrison and Poe tested *several* hypotheses that could explain sizes and patterns in female dewlap structures in *one genus* of lizard (*Anolis*) and merely could find no evidence that some of them, including species recognition, were in play in this particular case. This is not an invalidation of the general concept. On the other hand, Vanhooydonck et al. (2009) found that species recognition was one of the best hypotheses that explains dewlap patterns in both males and females of *A. sagrei*. Harrison and Poe concluded that much probably depends on the size of the habitat and the presence of other species, but the situation is complex and requires more study.

Beyond this, however, species recognition is understood to be important in the differentiation of lineages, both by itself and in conjunction with other processes. For example, in their influential review, Panhuis et al. (2001, p. 369) stated: “Species recognition is important when interpopulation or heterospecific mating is costly, producing relatively inviable or infertile offspring. Traits facilitating species recognition might then diverge under natural selection when populations or closely related species have overlapping geographical ranges.” And, in the same passage, “Several studies have shown (e.g. butterflies; fish and frogs) that male display traits can be both sexually selected and used in species recognition.”

Ritchie (2007), in another influential review in which he is fairly skeptical of the ability of sexual selection alone to cause speciation, notes that “[s]exual selection probably contributes most effectively alongside ecological selection or selection for species recognition than as a solitary process”, a view echoed by Panhuis et al. (2001). Ritchie (2007, p.83) further emphasizes that “[t]he issue of defining species recognition and sexual selection as different processes is critical when discussing speciation by reinforcement (selection against deleterious hybridization) or the evolution of behaviors to avoid signal

confusion or mating competition from heterospecifics. In these cases, behavior is evolving to be species-specific; therefore, species recognition is clearly a valid description of the function of the behavior.”

Even earlier, Ryan and Rand (1993) argued that species recognition and sexual selection may act in concert in the evolution of animal communication. Their discussion is highly nuanced and relevant here, because they recognize the importance of a phylogenetic legacy in the selection of certain behaviors involved in both mating and species recognition, a theme that we stressed (Padian and Horner, 2011a) in criticizing pan-adaptational hypotheses for “bizarre” structures in dinosaurs. For example, on occasions where female frogs preferred males of other species, Ryan and Rand note that it was because those males added a “chuck” to the ends of their calls that were not voiced by the males of the females’ species, but was a feature of the common ancestor of both species.

All of these cited authors point out, somewhat critically, that species recognition and sexual selection have often been treated either as antagonistic forces (a view they rightly reject) or as sites on a continuum (equally critically viewed) (Panhuis et al., 2001; Ritchie, 2007; Ryan and Rand, 1993). Much of this depends on the definitions of these terms (Ryan and Rand, 1993), which have been many (Mendelson and Shaw, 2012). Nevertheless, all these authors recognize the importance of the process of species recognition, especially in tandem with other processes. In Table 1, modified from Padian and Horner (2013) to include the concept of social selection, we argue that terms such as these are better understood not as part of a continuum but as a hierarchy (see below). We recognize, however, as Darwin (1871) did, that structures and behaviors can be used at more than one hierarchical level.

4. Claim 3. Even though species recognition has not been adequately studied in living animals, it is not “viable” for extinct animals

It is generally admitted that species recognition has not been adequately studied in living animals (Hone and Naish, 2013; Mendelson and Shaw, 2012; Padian and Horner, 2011a; Paterson, 1985), and that in studies where attempts have been made to assess it, there has been such a strong mate attraction signal entailed (or interpreted) with these behaviors that it has been difficult to tease apart (Panhuis et al., 2001; Ritchie, 2007; Ryan and Rand, 1993).

Main et al. (2005; see also Padian and Horner, 2011a) showed that hypotheses of mechanical function (adaptation) and various kinds of display frequently fail when trying to explain “bizarre structures” in extinct animals because either they are (a) untestable or (b) could not have worked in other members of that clade with similar structures (e.g., thermoregulation in all stegosaurs, jousting in all ceratopsids, sound amplification in all lambeosaurs). They proposed instead that these structures may have differentiated in closely related lineages and later served to reinforce species recognition among conspecifics (Fig. 1). Support for this came from two lines of evidence. First, members of a clade successively closer to the species with the adaptation in question (such as *Stegosaurus*) did not

Table 1

Hierarchy of concepts related to species recognition and mating. Each subcategory is subsumed within the one(s) above it, and therefore they are prerequisite to it (e.g., one must recognize possible potential mates before choosing among them); but the reverse does not necessarily hold true (e.g., mate choice does not necessarily require mate competition). There can also be competition for mates (e.g., zygotic) without active choice by either mate. Modified from Padian and Horner (2013).

Tableau 1

Hierarchie des concepts en liaison avec la reconnaissance de l'espèce et l'accouplement. Chaque sous-catégorie est sous-additionnée à celle(s) du dessus ; c'est pourquoi elle(s) lui est (sont) nécessaire(s) (c'est-à-dire qu'on doit reconnaître les partenaires potentiels possibles), mais l'inverse n'est pas nécessairement vrai (c'est-à-dire que le choix ne requiert pas nécessairement la compétition de partenaires). Il peut aussi y avoir compétition pour les partenaires (c'est-à-dire zygotiques) sans choix actif par l'un ou l'autre partenaire (modifié selon Padian et Horner, 2013).

Species recognition: the ability of individuals to recognize conspecifics for all relevant social purposes (cooperation, competition for resources, group behavior including colony formation, defense, etc.), and the processes by which they do so
Social selection: processes that select for and sort behaviors and recognition mechanisms that structure social functions in a species (mating, herding, mutual protection, social status, and other social behaviors)
Mate recognition: the ability of individuals to recognize what other individuals in their species are potential mates (e.g., in estrus), or even for gametes of opposite genders to recognize each other chemically, and the processes by which they do so
Mate choice: the processes by which individuals, presented with potential mates, decide actively on acceptance and rejection (includes mutual mate choice, often erroneously called "mutual sexual selection")
Mate competition: the process of competition for mates by members of the opposite sex
Sexual selection: the process of selection for traits possessed by one sex but not the other, or used by one sex and not the other, that increase access to mates by attracting them or by repelling rivals for mates

show progressive improvement in the proposed adaptation (Galton and Upchurch, 2004). Second, the expression of many "bizarre" features, such as the various accessory spikes and ornaments on the skulls of ceratopsids, show no obvious trends in morphology when the species are mapped phylogenetically. Main et al. (2005) hypothesized that these variations were favored and maintained in lineages as a way to reinforce specific distinction and to allow conspecific recognition.

A critical consideration, however, is the scale at which these evolutionary processes work. Main et al. (2005) and Padian and Horner (2011a, 2011b) emphasized that structures selected to enhance species recognition occur in lineages of closely related species. Hone and Naish (2013), in criticizing the potential importance of species recognition, erred at the level of phylogenetic scale in stating: "it is not at all clear that distribution of ornamentation (elaborate head, neck and tail feathering, wattles) is in any way 'directional' or phylogenetically 'logical'. Rather, ornamentation could be considered 'relatively random', albeit with members of specific lineages representing variations on a theme." Hone and Naish (2013, fig. 3) picked for their example a scattered sample of genera from the Phasianidae, which comprise some 150 living species representing lineages that have been diverging continually (Zhao et al., 2012) for at least 30 million years (Mayr et al., 2006). This is an inappropriate comparison to Mesozoic non-avian dinosaurs—first, because peafowl, pheasants, quail, grouse, turkeys, and other members of this group are a much larger and more long-lived clade than the closely related dinosaurs are, so species recognition is inappropriate to invoke at this taxonomic level; and second, these bird species are known to be highly sexually dimorphic, with the females and juveniles closely resembling those of related species. To draw a reasonable comparison to non-avian dinosaurs, it would be appropriate to use a group

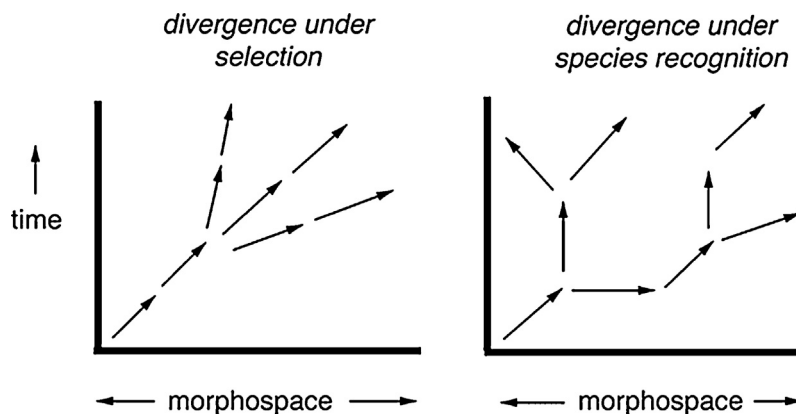


Fig. 1. Expected differences in macroevolutionary patterns of morphology between regimes governed by natural or sexual selection (left) and species recognition (right). Although these are extremes of a continuum of patterns, it would be expected that selection would cause more or less directional morphological trends through time as the function of a structure improved. But when species recognition is selected for, the object is to be recognizably different, not necessarily functionally better or more visually elaborate; so a range of morphology is possible, as long as the result is divergence. From Main et al. (2005).

Fig. 1. Différences attendues dans les diagrammes macro-évolutifs de morphologie entre régimes gouvernés par la sélection naturelle ou sexuelle (gauche) et par la reconnaissance de l'espèce (droite). Bien que ceux-ci constituent les extrêmes d'un continuum de diagrammes, il est attendu que la sélection induirait des tendances morphologiques plus ou moins directionnelles au cours du temps, comme la fonction améliorée d'une structure. Mais quand la reconnaissance de l'espèce est privilégiée, l'objet doit être différent de façon reconnaissable et non nécessairement meilleur du point de vue fonctionnel, ou plus élaboré du point de vue visuel ; ainsi, une gamme de morphologie est possible, tant que le résultat est la divergence (selon Main et al., 2005).

with distinct ornaments, but low or no sexual dimorphism, whose members have diversified only in the past few million years. That is what centrosaurine and chasmosaurine ceratopsians, pachycephalosaurs, and lambeosaurs did in the last few million years of the Late Cretaceous, independently and repeatedly (Horner et al., 1992).

5. Claim 4. Sexual selection does not require sexual dimorphism

This debate shows no sign of abating, regardless of historical precedent (Padian and Horner, 2011a, 2011b, 2013). It would seem necessary to establish two concepts of sexual selection: “Darwinian sexual selection” for what Darwin actually said when he established the concept, and “Neo-Darwinian sexual selection” to denote the alterations that distorted Darwin’s definition several decades ago and have confused many studies since then, including those by Hone and Naish (2013), Knell and Sampson (2011), Knell et al. (2012), and Hone et al. (2012).

During the 1970s, Darwin’s concept of sexual selection was radically altered by biologists who (we believe inadvertently) changed it from an explanation of why bizarre structures occur in one sex but not another (and that would be difficult to attribute to natural selection) to a mathematical description of reproductive success (see Padian and Horner, 2011b for a brief historical review). This revisionism is epitomized in Ryan and Rand’s (1993, among many other authors) definition of sexual selection as “variance in reproductive success that derives from variation in the ability to acquire mates”. But this merely reflects the confusion that is rife in today’s literature on sexual selection (Carranza, 2009; Clutton-Brock, 2007). There is no way out of this if biologists insist on describing every factor that increases mating success as “sexual selection.” More importantly, this disregard for history results in relegating to a minor role the main phenomenon for which the concept was invented.

Darwin (1859, 1871) established the concept of sexual selection not to describe differential reproductive success but to explain why bizarre structures were selected for in one sex, even though they provided no advantage to the survival of that individual. Such individuals would presumably have better access to mates (a testable hypothesis, not a dogma), and would leave not necessarily more offspring than others, but offspring that bore the same features that repelled rivals and attracted mates. Darwin knew exactly what he was doing. This is a complex concept that cannot be reduced to a mere advantage in fertility or production of offspring. And, despite the impression of many present-day workers, sexual selection cannot be “a kind of” natural selection (Padian and Horner, 2011b, 2013).

However, confusion is persistent. Knell et al. (2012), for example, claimed that “in neither *The Origin of Species* nor *The Descent of Man* can we find an unambiguous definition of sexual selection requiring sexual dimorphism.” Here is Darwin introducing the concept in the first part of the first edition of *The Origin* (1859: 89–90):

“Thus it is, as I believe, that when the males and females of any animal have the same general habits of life, but

differ in structure, colour, or ornament, such differences have been mainly caused by sexual selection; that is, *individual males have had, in successive generations, some slight advantage over other males, in their weapons, means of defence, or charms*; and have transmitted these advantages to their male offspring.” [emphasis added]

This could scarcely be clearer, and Darwin used more than 500 pages in *The Descent of Man*, and *Selection in Relation to Sex* (1871) to document what he was talking about. Large claws in beetles, antlers in cervids, horns in bovids, songs and feather colors in birds, dewlaps in lizards, and myriad other features are present in (usually) males but not females, and they are used to *repel rivals or attract mates* (Darwin, 1871), to the end of achieving greater access to mates. They may also be used in other contexts. Pursuant to the passage quoted above, Darwin (with his typical wisdom) noted that it is often difficult to tell whether a particular structure was shaped in the context of sexual selection or natural selection or both, and he realized that sometimes the females have the unusual structures; but he did not feel that his concept would fail based on these completely reasonable variations. What is critical is how the feature or behavior is used to gain access to mates.

(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. It is possible for larger males [e.g., in crocodiles] to use their size difference in repelling rivals and attracting mates, but if they also use it for greater success in trapping prey, then more information is needed to determine why it evolved or how it is maintained).

The situation is considerably worse for extinct animals. Knell et al. (2012) maintained that “Many fossil animals bear traits such as crests or horns that *probably functioned as sexually selected signals* or weapons. Interpretations of these structures as functioning in mate choice or intrasexual contests are often controversial, with interpretations based on biomechanics or physiology being favoured by many. Although testing hypotheses based on sexual selection can be difficult, especially given that *there is no single, reliable means of recognising sexual selection*, we argue that it is not impossible; indeed, *there are now several cases where sexual selection is strongly supported*.” (emphasis ours). This passage shows the confusion that ensues when Darwin’s definition of sexual selection is ignored: sexual selection means whatever one wants it to mean, and notions of what is “probable” or “supported” have no objective testability.

We have previously (Main et al., 2005; Padian and Horner, 2011a, 2011b, 2013) shown that although Darwinian sexual selection is well established in many clades of living animals, its application to extinct dinosaurs and their relatives is unsubstantiated. We base this on the absence of any evidence that these taxa showed Darwin’s requirement of sexual dimorphism. Most recent authors who have discussed sexual selection in extinct animals (Hone and Naish 2013; Knell et al., 2012) accept the Neo-Darwinian view that sexual dimorphism is not required for sexual selection; however, Darwin invented the concept to

explain unusual dimorphic structures, not to provide yet another measure of numbers of offspring left in the next generation.

Various reasons are offered for why it is permissible to change the definition of a concept. Knell et al. (2012) argue that we have learned a lot since Darwin's time, and therefore we are entitled to alter his definitions. Darwin, after all, did not know everything. Of course, no one does, but it is astonishing how much Darwin perceived beyond others in his day and how well so many of his concepts remain valid, including his original formulation of sexual selection. Those who think it is fair game to alter definitions based on recent reformulations of concepts fall into Humpty Dumpty's trap (Carroll, 1871): "When I use a word, 'Humpty Dumpty said in rather a scornful tone,' it means just what I choose it to mean — neither more nor less." This quotation is sometimes mistakenly ascribed to Carroll's Red Queen; but of course, the Red Queen learned herself that in evolutionary biology, her original formulation by Van Valen (1973) as a statement of how all organisms compete for diffuse forms of energy could be transformed into an emblem of sexual competition (Bell, 1982) and even dichotomized into the relative influences of biotic and abiotic factors on evolution (Barnosky, 2001). There is nothing wrong with this research, but it distorts and distracts from the original formulation of the concept, which was of at least equal value.

Hone and Naish (see also Knell et al., 2012) point to concepts such as sperm competition and "mutual sexual selection" to show how the understanding of sexual selection has "improved" since Darwin's time, and therefore that we should feel no obligation to honor his definition. Sperm competition is uncontroversial as an example of sexual selection, because the males have structures that the females lack, and they use them to repel rivals (in this case, to remove sperm previously deposited by other males and therefore to deny them access to the female's reproductive system), which is just what Darwin was talking about. Finding new examples does not invalidate a definition.

As for "mutual sexual selection," Darwin never used the term (*contra* Jones and Hunter, 1993, and others). Darwin knew that there were some species that had exaggerated structures in both sexes (cassowaries, for example). He excluded them from his concept of sexual selection. This is because he needed to explain bizarre structures that were in one sex and not the other. This is why "mutual sexual selection" is an oxymoron. 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. The concept of "mutual sexual selection" is best restated as "mutual mate choice." (Mate choice does not equal sexual selection: Table 1). Moreover, the structures used in mutual mate choice could be the same as those that facilitate species recognition. There is no evidence that these structures were *specifically selected* as aids to repel rivals (which both males and females would have to use) or attract mates. In most cases it is simply assumed that this is what they are used for. Jones and Hunter (1993), in their classic study, showed

experimentally that both sexes of the crested auklet prefer larger crests to artificially shortened ones (i.e., mutual mate choice), although they did not (and perhaps could not) test whether these preferences actually shaped the evolution of the crest.

Studies of extinct tetrapods (Hone and Naish, 2013; Hone et al., 2012; Knell et al., 2012; Tomkins et al., 2010) that tout sexual selection have no experimental evidence and have not tested alternative hypotheses. These authors use "mutual sexual selection" as a default hypothesis based on poorly constrained analogy to isolated living examples in which "mutual sexual selection" (i.e., mutual mate choice) has not even been adequately established. Could these dinosaurs have used their bizarre structures in mutual mate choice? We have no objection to the hypothesis, but it cannot be *directly* tested any more than species recognition can, and neither one can be regarded as a "default hypothesis." Indirect diagnostic tests of "mutual sexual selection" are still wanting.

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 (Table 1). Reducing the concept to "success in reproduction related to success in obtaining mates" guts Darwin's entire theory of how bizarre, non-adaptive (and even maladaptive) structures evolve in one sex and not the other, a concept he needed to stave off objections that not all structures were shaped by natural selection (Padian and Horner, 2011a, 2011b). To follow the "Neo-Darwinian" course leaves no term for the very important class of observations that Darwin (1871) documented so copiously.

6. Claim 5. The two proposed tests of species recognition fail in the cases of Cretaceous dinosaurs

Main et al. (2005) and Padian and Horner (2011a) proposed, first, that under species recognition, sister species diverging in sympatry (or close allopatry) would be expected to show little in the way of directional trends, compared to traits under natural selection or sexual selection. This mechanism was discussed above. Hone and Naish (2013), following some traditional authors, claimed that the bizarre features of non-avian dinosaurs showed trends in evolution that "could well be interpreted as representing" functional improvement or sexual selection, but they provided no evidence for this claim.

The second proposed test was that, under selection for species recognition, apparently "random" character divergences would be expected to occur in closely related sympatric lineages. Under selection for species recognition there is no obligation but to be different in some respect from closely related populations that are sympatric or parapatric; some lineages may even do this without trying to differentiate themselves from neighboring populations (e.g., *Triceratops*, stegosaurs, and many populations of living birds; see below).

Hone and Naish (2013) bring up a case of stegosaurs with poorly resolved taxonomy and phylogenetic relationships and claim that this is evidence against species

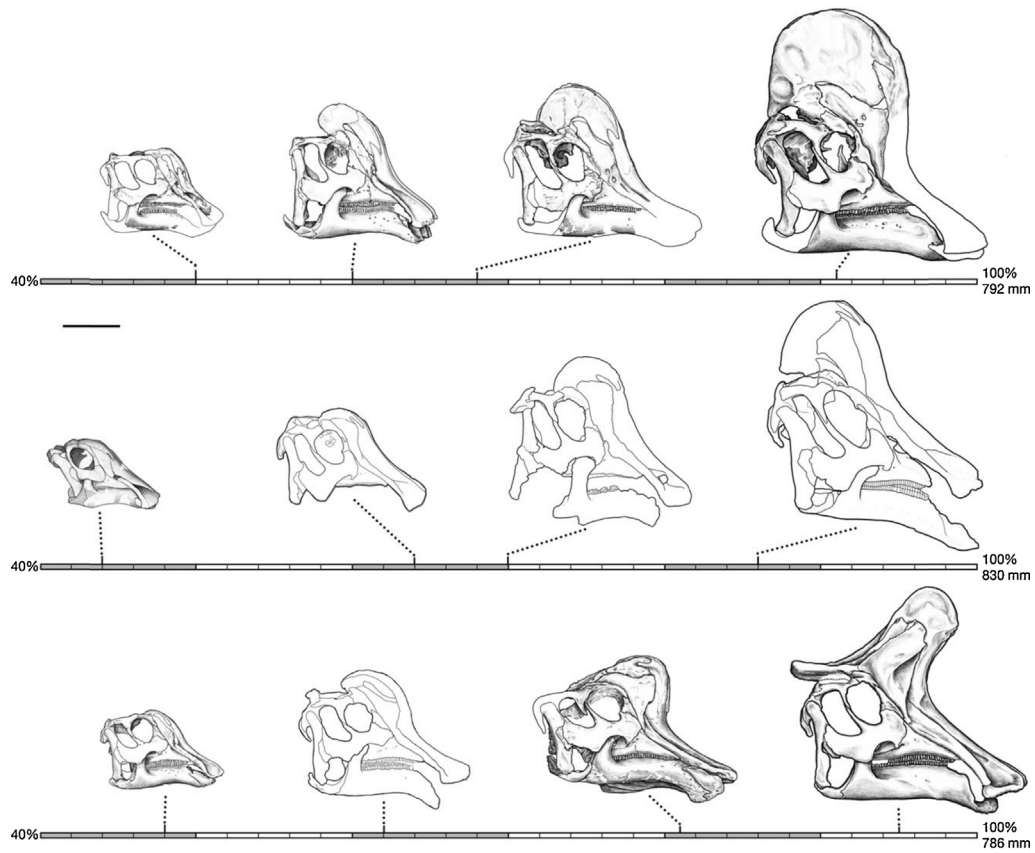


Fig. 2. Hypothetical cranial growth series of *Corythosaurus casuarius* (top), *Hypacrosaurus altispinus* (middle), and *Lambeosaurus lambei* (bottom), drawn approximately to scale. The individual specimens are positioned on the corresponding scale according to their percentage of maximum observed skull length. Scale bar: 20 cm. From Evans, 2010, used by permission.

Fig. 2. Série hypothétique de croissance crânienne chez *Corythosaurus casuarius* (en haut), *Hypacrosaurus altispinus* (au milieu) et *Lambeosaurus lambei* (en bas), dessinée approximativement à l'échelle. Les spécimens individuels sont positionnés sur l'échelle correspondante, selon le pourcentage du maximum de longueur du crâne observé. Barre d'échelle : 20 cm (selon Evans, 2010, avec son autorisation).

recognition; we suspect that if the taxonomists have not yet figured out what names to use, the material is inadequate or their approaches to it are. They also claim that “[a]n additional argument against the use of exaggerated structures in species recognition is that some structures differ little between sympatric species.” Of course; cryptic sympatric or parapatric species are found all the time, and see Hutchinson (1959) for a classic example of Italian water beetles. But this is beside the point. It is also difficult to understand the evidence (if any) for their claim that “[i]f the primary selective process driving the presence of such structures was species recognition, we would predict that species would differ with respect to the form of a single structure—additional or elaborate structures would be redundant and pose additional costs.” We address “costs” below.

Turning to the empirical evidence (Horner et al., 1992; Scannella and Horner, 2010; Weishampel, 2007), it is easily seen that, at any given time in the Late Cretaceous of the North American Western Interior, several closely related taxa of chasmosaurine and centrosaurine ceratopsians were sympatric or parapatric. They differ mainly in

the minor “bells and whistles” features of their frills and horns, just as we would predict.

Among crested hadrosaur (lambeosaurines), *Corythosaurus* and *Lambeosaurus* show a similar differentiation (Fig. 2, from Evans, 2010), and these taxa may have “morphed” stratigraphically into other distinct forms, just as we have seen with *Triceratops* (Scannella and Horner, 2010; see also Horner et al., 1992). Again, no sexual dimorphism is found. However, in sharp contrast to *Triceratops* (Goodwin et al., 2006), in most lambeosaurines the specifically distinct crest features do not begin to develop until the animals reach at least half of their linear growth (by which we presume that they are sexually mature), and they have not yet differentiated into species-specific forms (Evans, 2010). The crests do not become close to fully elaborated until the animals reach 80–90% of their full size, well past the initiation of sexual maturity (Fig. 2). And again, no sexual dimorphism is found. If these features were under “mutual sexual selection” they would have developed much earlier. We hypothesize that these animals were gregarious and that the elaboration of the crests reflects social status as much as species recognition.

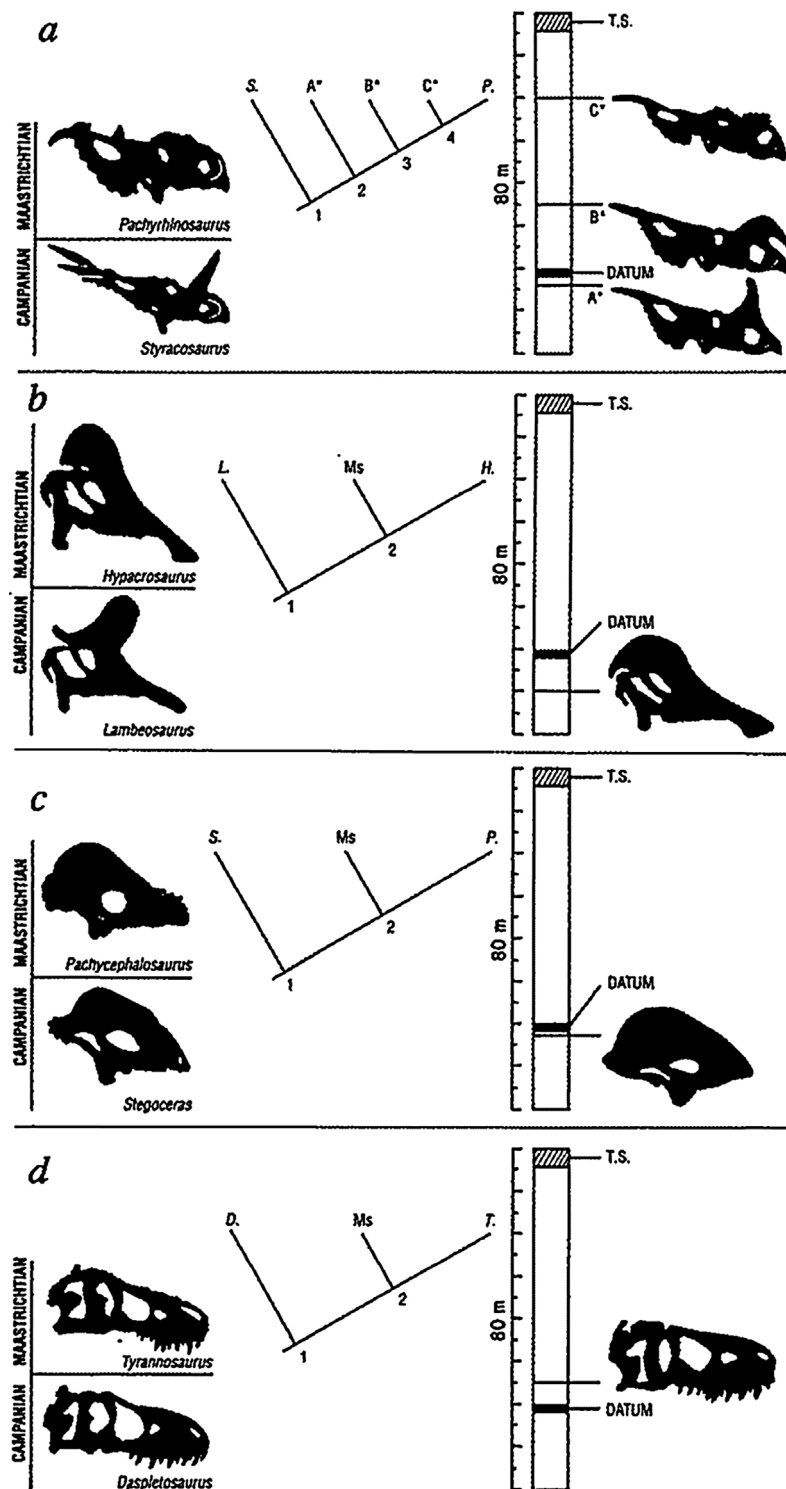


Fig. 3. Cladograms (not phylogenies) and stratigraphic columns showing cladistic clustering and stratigraphic positions of intermediate taxa of dinosaurs in the Late Cretaceous of the North American Western Interior. Drawings on left represent taxa proposed to be linked by taxa with intermediate features (right). Stratigraphic columns on right represent the uppermost 80 m of the Two Medicine Formation (Campanian). TS represents the “transitional sediments” of the Bearpaw Shale. For details, see [Horner et al. \(1992\)](#).

Fig. 3. Cladogrammes (et non phylogénies) et colonnes stratigraphiques montrant le groupement cladistique et les positions stratigraphiques des taxa intermédiaires de dinosaures du Crétacé récent du Western Interior nord-américain. Les dessins de gauche représentent les taxa dont on propose qu'ils soient reliés par des taxa à traits intermédiaires (à droite). Les colonnes stratigraphiques de droite représentent les 80 m supérieurs de la Formation Two Medicine (Campanien). TS représente les « sédiments transitionnels » du Bearpaw Shale. Pour plus de détails, voir [Horner et al. \(1992\)](#).

Horner et al. (1992) described an exceptional constellation of Cretaceous dinosaurs (ceratopsians, lambeosaurs, pachycephalosaurs, and tyrannosaurs) from the Western Interior of the US that showed apparently anagenetic transformations in cranial ornamentations. Fig. 3 shows the stratigraphic positions of these successive forms, which again do not show sexual dimorphism but do include transitional individuals. The figures treat the specimens as if they were distinct species (i.e., in a cladistic analysis, which is not a phylogeny and cannot show possible linear transitions), but Horner et al. explained in their text that the transitions were real: “Anagenesis, rarely documented in terrestrial vertebrates and almost unknown in Mesozoic vertebrates, seems to be clearly evident in these dinosaurs.” It is clear that these transitions could occur quickly and that some forms had sympatric relatives. Given the lack of sexual dimorphism it is difficult to see how sexual selection could be involved, but the closely tracked changes in morphology speak directly to species recognition and coherence.

7. Claim 6. The “ontogenetic morphing hypothesis” (OMH) of some dinosaur groups is evidence against species recognition

Scannella and Horner (2010), following the lead of earlier authors, were able to reduce some 18 named taxa of *Triceratops* and *Torosaurus* to ontogenetic stages of a single lineage, represented by two species that succeed each other in time, and with no sexual dimorphism. Using new discoveries of dozens of specimens closely tied to stratigraphic position, they found that *Triceratops prorsus* is succeeded by *T. horridus* in the Hell Creek Formation (Maastrichtian, US Western Interior), and that *Torosaurus* is an adult form of *Triceratops* (Goodwin et al., 2006; Horner and Goodwin, 2006). Hone and Naish (2013) argue that other authors (Farke, 2011; Longrich and Field, 2012) dispute this interpretation, but Scannella and Horner (2010) showed that the putative autapomorphies of “Nedoceratops” that Farke (2011) provided (to argue that the specimen represented a different species) were also found in other specimens of *Triceratops*, and also that the skull in question had severe pathologies. Longrich and Field (2012) used only 36 specimens with no stratigraphic or geographic control, and evaluated the relative ontogenetic age of their specimens by eye, rather than histologically (in contrast to Horner et al., 2011). It will be interesting to see if other authors can falsify the OMH, or support a different hypothesis, after they perform a full analysis of all the data, including a much larger sample size with precise stratigraphic and geographic control. Such a study was performed by Horner et al. (2011), reporting the results of over a decade of fieldwork in the Hell Creek formation that obtained over 240 articulated or associated dinosaur specimens of seven taxa, all recorded in precise geographic and stratigraphic context. We note that even in the limited sample (36 individuals) studied by Longrich and Field (2012), their fig. 5 shows that five of the six specimens attributed to *Torosaurus* fall into their “adult” category, and the sixth is a very large “sub-adult” (their characterizations), which actually supports the OMH.

Hone and Naish (2013) claim that the unusual non-linear allometry of many features of these ceratopsian skulls, which were interpreted in the context of “status recognition” of different ontogenetic stages (Horner and Goodwin, 2006; Padian and Horner, 2011a), do not support species recognition, but they are conflating two kinds of differences. Some characteristics are diagnostic of individual species, but other characteristics diagnose ontogenetic stages. Non-avian dinosaurs achieved sexual maturity before completing skeletal growth—in fact, by about two-thirds of their adult linear size and half of their adult mass (as recognized by the formation of an External Fundamental System: see Horner and Padian, 2004; Lee and Werning, 2008; Schweitzer et al., 2005). Although Hone and Naish (2013) claimed that “[c]orrectly identifying a conspecific of the correct status (social or reproductive) gets harder, not easier, when several transforming morphs are present,” it really does become easier, because there are more intermediate stages in an increased sample, and the ontogenetic stage of individuals can be assessed independently by histology. The growth patterns suggest that some features could advertise sexual maturity and some could advertise social status, and that they are not mutually exclusive.

8. Conclusion: The roles of sexual selection and species recognition in animal behavior

In Table 1 (modified from Padian and Horner, 2013 to include social selection), we describe how intraspecific behaviors related to mating and other functions are hierarchical. It seems self-evident that it is not possible to choose a mate among possible mates until and unless conspecifics have been identified. This means that species recognition is prefatory to other intraspecific activities, although species recognition *per se* has not been studied in most animals in which mating behavior has been. Some biologists maintain that this process is not important, and should only be considered when an individual makes “mistakes” in mating with a non-conspecific, creating a “cost.” In graphic terms, a dog can attempt in vain to mate with another male dog, a fire hydrant, or his owner’s leg; but a day, two days, or several hours later he may encounter a receptive female and achieve procreation. Is there really a “cost” of this profligacy? Can it be calculated, or is it just hypothetical modeling based on mathematical assumptions? Can the innate ability to recognize conspecifics be unimportant? In the end, animals congregate with others of their species for reasons other than reproduction, and that presumes that they know who is in their species.

The general issue of “cost” of advertising features for species and (or) mate recognition seems to be an argument rooted more in theoretical speculation than in practice. This is not to say that organisms suffer no “costs” of metabolic and sexual activity, but such alleged “costs” cannot be assumed to be debilitating, especially when lineages have been successful for long periods. Whether neoceratopsians, for example, evolved their horns, frills, and other adornments in the context of mate recognition or mate choice or of species recognition (or some combination thereof), they devoted metabolic effort to developing and reworking these structures ontogenetically. But obviously, as for

many other lineages, it worked fine for them over millions of years.

“Costs” of reproduction sometimes seem outlandish, but they are apparently not excessive to the animals. Take the innumerable species of marine crustaceans that broadcast their eggs and sperm into the water column. What is the “cost” of the waste of hundreds of thousands of gametes merely to replace a breeding pair? These clades have survived and prospered for hundreds of millions of years. An Irish Elk male typically grew and shed 20 kg of antler bone each year. Did the lineage become extinct from metabolic exhaustion? “Cost-benefit” arguments at these levels are spurious.

Among animals that actively seek and choose mates, [Table 1](#) suggests that one normally differentiates which members of the opposite sex are appropriate mates, then chooses among them based on various characteristics. One may simply take the first possible mate to hand, in which case mate choice is not so important. The same is true with mate competition: it may be important or not in a given situation.

Sexual selection, as Darwin invented it, is only a small part of this whole complex of behaviors. There must first be mate recognition, mate choice, and mate competition. Here, the competition is of a very particular kind. 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. But it is not universal in the struggle to acquire mates, and should not be synonymized with any general sort of competition for mates or of processes of mate choice.

One may, of course, maintain that [Darwin \(1859, 1871\)](#) did not know what he was talking about, or was vague about his concepts, or that his examples were inconsistent (the animal kingdom is complex). But historians recognize that he devised the concept of sexual selection to explain the “bizarre structures” that (usually) males of some species had and that the females lacked, and that were used to attract mates and repel rivals. This explanation was critical to answering skeptics of his theory of natural selection, who could have rightfully claimed that structures such as the peacock’s tail could not have evolved under natural selection to improve the adaptive fitness of its bearer. We think that not all intraspecific sexual interactions should be labeled “sexual selection.” We do not think it is acceptable to assert by analogy alone that superficially similar structures in living and extinct animals were shaped by sexual selection, without being obliged to test this hypothesis or others ([Knell et al., 2012](#)). Analogy is not a test of anything. It is merely a rhetorical device.

Species recognition is a viable hypothesis to explain many “bizarre structures” in non-avian dinosaurs because the differences among closely related contemporaneous and sympatric or parapatric species are non-adaptive, non-directional in their trends, and non-dimorphic. No other hypothesis explains these features better, and all have substantial flaws ([Padian and Horner, 2011a, 2011b](#)). Corrupted definitions and inattention to the history of the field of evolutionary biology have brought confusion to what can be sorted out, if the profusion of

conflicting descriptions of concepts is replaced by a sensible hierarchy ([Table 1](#)).

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