REVIEW

The 'species recognition hypothesis' does not explain the presence and evolution of exaggerated structures in non-avialan dinosaurs

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Abstract

The hypothesis that the exaggerated structures in various non-avialan dinosaurs (e.g. horns, crests, plates) primarily functioned in species recognition, allowing individuals of a species to recognize one another, is critically examined. While multifunctionality for many such structures is probable given extant analogues, 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. Furthermore, some of the evidence presented does not support the hypothesis as claimed or is equivocal or erroneous. Suggestions that certain evolutionary patterns of diversification in these exaggerated structures are indicative of a role in species recognition are unreliable, as both a degree of phylogenetic directionality and of randomness are seen in extant species where similar structures function in sexual selection. Claims that an absence of sexual dimorphism in the exaggerated structures of non-avialan dinosaurs rule against a role in sexual selection ignores the possible existence of mutual sexual selection and is also sometimes limited in view of sample sizes. The suggestion that the existence of species recognition is supported by the presence of exaggerated structures in sympatric, closely related relatives is also erroneous because adorned dinosaur species sometimes exist in the absence of unadorned relatives. We conclude that species recognition was not the evolutionary mechanism most likely to be driving the appearance and persistence of exaggerated structures in non-avialan dinosaurs.

Introduction

The non-avialan dinosaurs of the Mesozoic (i.e. all dinosaurs except the members of the bird lineage) are well known for the many exaggerated structures present in members of numerous lineages. These include ceratopsian frills and horns, pachycephalosaur skull domes, hadrosaur cranial crests, the cranial hornlets, bosses and ridges of various theropods, elongate neural spines in ornithopods, theropods and sauropods, and plates, spines and spikes on the heads and bodies of thyreophorans (Fig. 1) (see Hone, Naish & Cuthill, 2012).

Traditionally, these structures have been interpreted within 'functional' or 'mechanical' hypotheses, supposedly playing roles in thermoregulation, inter- and intraspecific combat and/or self-defence (see Hone *et al.*, 2012 for a review). These functional proposals, while representing valid hypotheses, have either failed to withstand scrutiny (e.g. Dodson, 1976; Main *et al.*, 2005), or remain equivocal

(Farlow, Hayashi & Tattersall, 2010). Modern studies have emphasized the probable multifunctionality of these structures: Farke, Wolff & Tanke (2009), for example, argued that intraspecific combat was likely only one among several functions contributing to horn and frill evolution in ceratopsids, while in sauropods, Taylor *et al.* (2011) noted that use of the neck in foraging did not exclude a possible role in sexual selection.

An improved understanding of the biology of display structures and sociosexual behaviour in extant animals, coupled with the realization that fossil animals must have been subject to the same selection pressures as extant ones, means that many workers favour sociosexual selection as the primary mechanism driving the evolution of these structures in non-avialan dinosaurs (e.g. Farlow & Dodson, 1975; Hopson, 1975; Hone *et al.*, 2012; Knell *et al.*, 2013). These features could be used intraspecifically in advertising fitness (e.g. Spassov, 1979; Hayashi, Carpenter & Suzuki, 2009; Tomkins
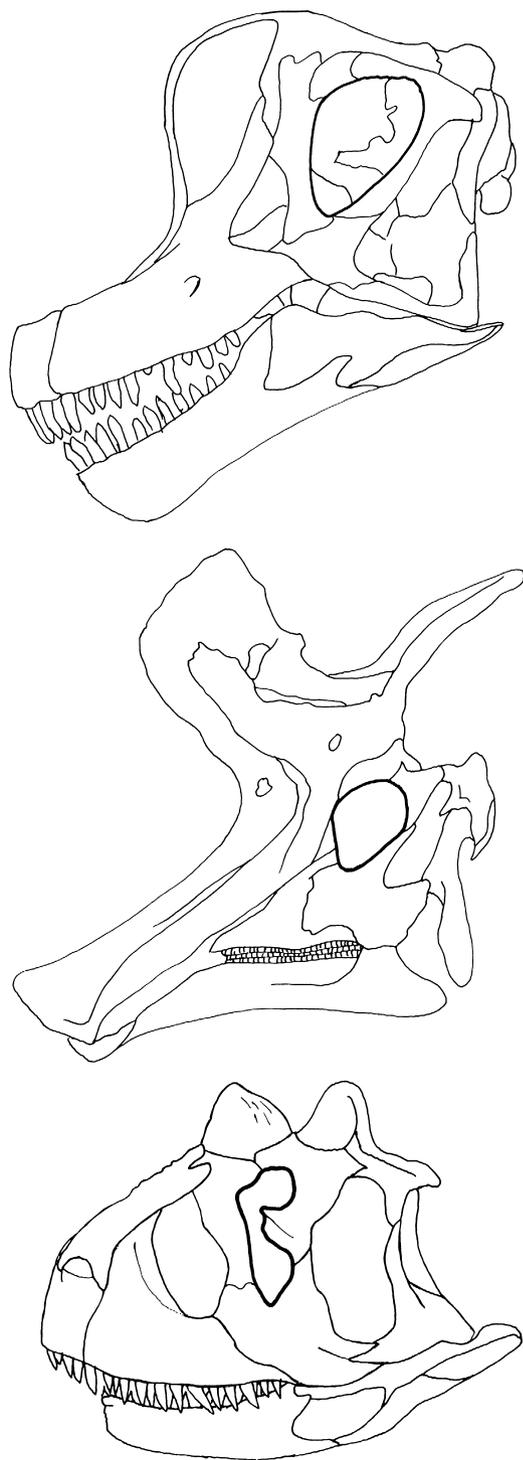
Figure 1 The skulls of a selection of dinosaurs with exaggerated cranial structures. Top to bottom: the brachiosaurid sauropod *Giraffatitan* with an enlarged narial bar, the hadrosaur *Lambeosaurus* with a large cranial crest (both based on Norman 1991), and the abelisaurid theropod *Carnotaurus* showing a pair of horns over the eyes (based on Bonaparte *et al*. 1990). Images are in left lateral view and not to scale.

et al., 2010), as advertisers of social status, and in intraspecific control of resources (Hieronymus *et al*., 2009).

A lack of convincing dimorphism across many such exaggerated structures has led some authors to reject sexual selection as an explanation for their evolution (Padian & Horner, 2011*a*), despite concern about the small sample sizes involved. Even if sexual dimorphism is demonstrably absent, a rejection of sexual selection ignores the possible presence of mutual sexual selection, the phenomenon – well studied and well established in extant animals – in which both genders are ornamented (see Hone *et al*., 2012 and references therein). The assumption that an absence of sexual dimorphism is incongruous with sexual selection also ignores the possibility that exaggerated structures could function as other kinds of social dominance signals relevant to both genders. Instead, it has repeatedly been suggested that exaggerated structures in non-avialan dinosaurs may have functioned as species recognition devices (e.g. Main *et al*., 2005; Hieronymus *et al*., 2009; Padian & Horner, 2011*a*; Allain *et al*., 2012; Schott & Evans, 2012; Taylor & Wedel, 2012). This is despite the fact that similar structures in extant vertebrates have roles in sexual selection (Knell *et al*., 2013) and the lack of evidence for species recognition.

The term 'species recognition' has been applied to different concepts by different authors and there is little consistency in its use (Mendelson & Shaw, 2012). Padian & Horner (2011*a*) noted that 'functions of species recognition encompass interactions both between species (discourage association of non-conspecifics) and within species ("encourage association of conspecifics")'. However, while these two aspects of behaviour are linked (the second is generally termed 'social selection'; West-Eberhard, 1983), the former is closer to interspecific signalling and need not have any effect on conspecifics. Moreover, 'species recognition' may refer to the behaviour whereby individuals identify and keep track of conspecifics for herd coherence, or identify a suitable sexual partner. These two behaviours need not be mutually exclusive; however, they may be associated with different selective pressures. Consequently, we split this concept into 'herd recognition' and 'mate recognition' and use the term 'species recognition' only when both phenomena are implied. Note that Padian & Horner (2011*a*) considered mate recognition a subset of species recognition, although our distinction is somewhat different. Wider questions exist for definitions of species recognition (Mendelson & Shaw, 2012) and related factors (such as 'competitor recognition' – Losos, 1985); here we restrict ourselves to those definitions used in the context of discussions about exaggerated structures in non-avialan dinosaurs.

The sexual selection and species recognition hypotheses have been framed as alternatives (Main *et al*., 2005), but they are not mutually exclusive. Exaggerated structures of the sort seen in non-avialan dinosaurs can of course be multifunctional, as they often are in extant taxa (e.g. elephant tusks, deer antlers). Hypothetically, a crest could simultaneously serve as a sexual signal and as an aid to social cohesion, while also functioning as a threat to a predator or other heterospecific, and as a signal used to identify prospective mates in addition to a mechanical function such as combat. Despite
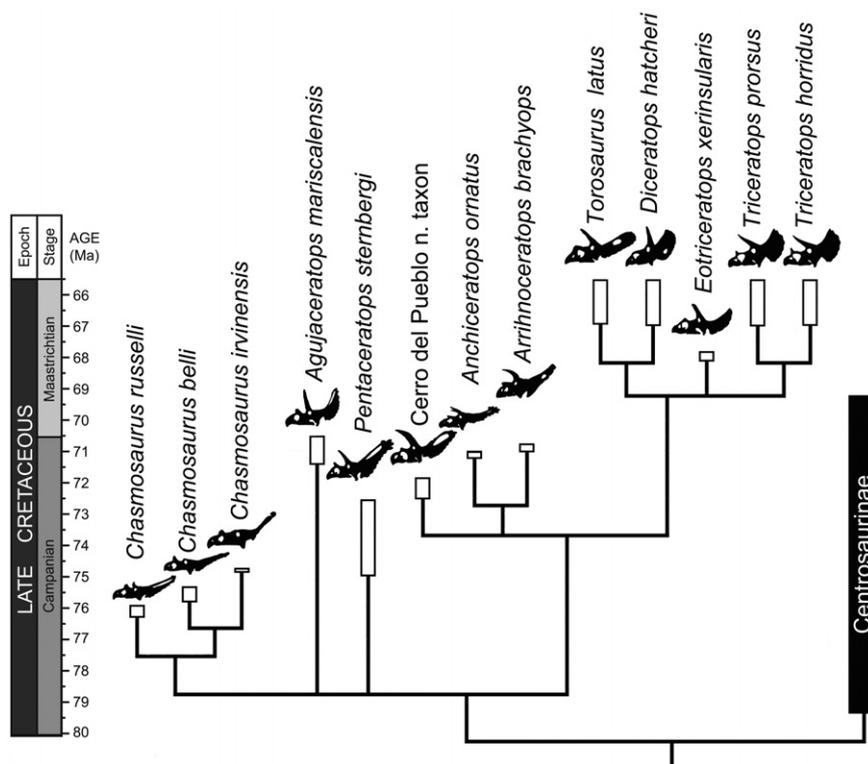
Figure 2 Simplified, time-calibrated phylogeny of chasmosaurine dinosaurs showing their skulls, modified from Sampson & Loewen (2010). Several trends observed across the phylogeny are consistent with an 'improvement of a function' or 'continued trend in mate selection' (see text for discussion). A modified version of the topology shown here has since been published by Sampson *et al.* (2010). *Chasmosaurus irvinensis* is now known as *Vegaceratops irvinensis* and the 'Cerro del Pueblo n. taxon' has since been named *Coahuliceratops magnacuerna*.

this, we would hypothesize that one function likely dominates the origins and primary selective pressure driving the evolution of a structure, even if later co-option occurs.

It is undeniable that exaggerated structures would help individual dinosaurs identify conspecifics (or distinguish heterospecifics). The issue is whether species recognition (depending on its definition) was the primary mechanism driving the acquisition or maintenance of any, or all, of these structures, or that species recognition would produce the hypothesized effects (e.g. speciation, large adornments).

Discussion

Our discussion here is limited to the available morphological data, although it should be noted that non-avialan dinosaurs were likely similar to extant animals and probably used multiple signals as identifiers. These could potentially have included smell, colour, behaviour, soft tissue structures or any combination thereof. Such identifiers may be considered close to 'zero-cost' signals (Knell & Sampson, 2011); indeed, with respect to integument, differences in scalation patterns are known for at least some sympatric dinosaurian taxa (see Bell, 2012). Padian & Horner (2011a) provided two observations purported to support the species recognition hypothesis, and also put forward two accompanying tests designed to determine whether structures might have evolved under the selective pressures of a species recognition function. First, they advocated that a lack of directional evolution in the expression of an exaggerated trait argues for that trait's role in

species recognition (see also Main *et al.*, 2005; Hieronymus *et al.*, 2009). Second, they argued that the presence of such traits in sympatric, closely related taxa supports their role in species recognition.

Observation 1

Padian & Horner (2011a) argued that a 'relatively random' pattern of diversification in exaggerated structures (where there is no obvious directional trend in the evolution of the respective structures) better fits the species recognition hypothesis than others. We suggest that within the most elaborately adorned non-avialan dinosaurs (lambeosaurine hadrosaurs and ceratopsids), closely related taxa represent variations on a theme, not random divergences from an ancestral bauplan. Phylogenies of centrosaurine ceratopsids, for example, reveal several trends in evolution that could well be interpreted as representing 'improvement of a function (natural selection) or continued trends in mate selection (sexual selection)' (Padian & Horner, 2011a). These include the reduction of brow horns and their replacement by supraorbital craters, the replacement of brow horns with bosses and the subsequent anterior enlargement of these bosses, and a trend in which the nasal horn shortens and is replaced by a boss and associated novelties (Currie, Langston & Tanke, 2008; Fiorillo & Tykoski, 2012) (Fig. 2).

However, at least some sexually selected structures in extant taxa are known to have high levels of variation (Alatalo, Höglung & Lundberg, 1988; Fitzpatrick, 1997;
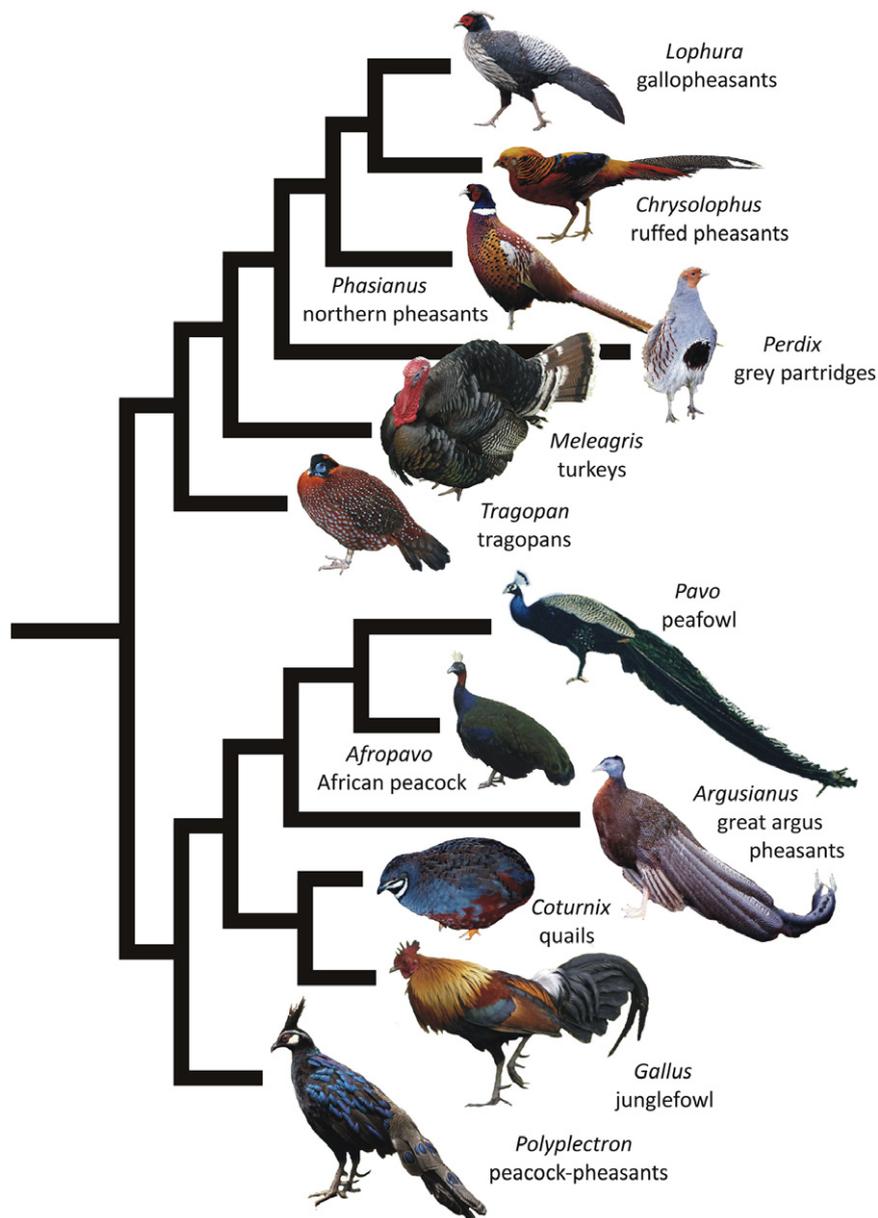
Figure 3 Simplified partial phylogeny of gamebirds, based on molecular tree in Bonilla *et al.* (2010). Gamebird phylogenies reveal few overall trends in the evolution of ornamentation (including facial wattles, neck hackles, uppertail coverts etc); rather, ornamentation frequently appears random and autapomorphic with independent losses and gains of ornamentation being frequent. Image sources are listed in the acknowledgements.

Emlen *et al.*, 2012) and may evolve at random; indeed, any neutrally selected character may evolve randomly. As argued by Knell & Sampson (2011), 'obvious directional trends' are not clearly present in those extant lineages where sexual selection seems to be primary mechanism driving the evolution of exaggerated structures. Knell & Sampson (2011) used beetles as examples, but the same argument applies to extant dinosaurs: gamebird phylogenies, for example (Kriegs *et al.*, 2007; Huang *et al.*, 2009; Bonilla, Braun & Kimball, 2010), reveal that 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 (Fig. 3).

Similarly, Hieronymus *et al.* (2009) suggested that a lack of dimorphism should be interpreted as an indicator of species recognition. Even leaving aside the fact that mutual sexual selection invalidates this argument (or at least provides an alternative; see Hone *et al.*, 2012), and leaving aside the continual problem of sample size, this logic is flawed. Males and females may suffer different penalties for 'incorrect' mating, meaning that they are under different pressures when identifying mates, and thus subject to potentially dimorphic signals. Similarly, males and females may be under different social regimes, meaning that evolutionary pressure could promote

dimorphism in signals. For example, females may need to be recognized by their young when males do not, and males may form bachelor herds when females do not. Thus while males and females would need to identify each other to breed, they would not necessarily need to recognize conspecifics of the opposite sex outside the mating season. Dimorphism might therefore be expected for some taxa if the herd recognition hypothesis was correct.

To conclude, neither the presence of a fairly random pattern of diversification in exaggerated structures, nor the lack of sexual dimorphism, represent clear support for the species recognition hypothesis over others.

Observation 2

Padian & Horner (2011a) argued that the presence of exaggerated structures in sympatric, closely related taxa supports their role in species recognition. However, it has been noted that 'mating signals of sympatric species often are more distinct from one another than are other signals produced by the same species' and, furthermore, that 'species confined to different regions have no possibility of confusing their signals' (both quotes by Wells & Henry, 1998). In short, we would expect that if these features functioned in species recognition, they would be more divergent between sympatric species, and less divergent between allopatric ones. However, this is clearly not true for a number of examples in the dinosaur fossil record.

Wuerhosaurus (or *Stegosaurus*) *homheni* is the only stegosaur recognized in the Lower Cretaceous Lianmuging Formation of China (Maidment *et al.*, 2008). Given the distinctive bauplan of stegosaurs relative to potential sympatric dinosaurs, it is unlikely that individuals would struggle to identify conspecifics simply because they lacked dorsal plates and tail spikes. This and other examples (e.g. the lone Asian spinosaurine, *Ichthyovenator*, Allain *et al.*, 2012) render it difficult to interpret species recognition as a viable primary explanation for the evolution of exaggerated structures among these taxa. Main *et al.* (2005) noted of stegosaur anatomy that while 'we have no independent evidence of mate competition, we can use the features of their plates to identify species'. However, this is not always true: disagreement continues over stegosaur taxonomy, with variation in plate and spike form being interpreted as within intraspecific variation by some, but exceeding it by others (Maidment *et al.*, 2008). Similar problems exist for other lineages.

An additional argument against the use of exaggerated structures in species recognition is that some structures differ little between sympatric species. The Upper Cretaceous Inner Mongolian locality of Bayan Mandahu, for example, has yielded the apparently contemporaneous neoceratopsians *Protoceratops hellenikorhinus*, *Bagaceratops rozhdestvenskyi* and *Magnirostris dodsoni* (Lambert *et al.*, 2001). If some of these taxa are synonymous, then likely only one species occupied any one locality at any one time, and we return to the paradox of a character for 'species recognition' when there is no possibility of confusion. Alternatively, if there are several species here, how do they distinguish one another based on their frills and bosses? Their morphology is so similar as to

confuse and confound taxonomists (note that frill and boss characters are not always included in the diagnoses of these taxa, as they are not unambiguously distinct), leaving us to wonder how the animals themselves might identify conspecifics if externally visible morphology was their only guide. The species concerned are in fact conservative in the area of morphology supposed to help separate them and make them distinctive, despite the variety of form seen in the frills and horns of other ceratopsians.

In this case, the exaggerated structures are not unique to specific taxa and do not 'involve a shift in morphology . . . that are not only visible to conspecifics and members of the parent species, but may also be visible to us' (Vrba, 1984) and nor do they fit the claims of Padian & Horner (2011b) that such taxa should 'evolve so as to differentiate themselves from other species, not from members of their same species'. Ironically, Main *et al.* (2005) recognized this, stating that there should 'be an advantage in differentiating one's recognition signals from those of related congeners'. We agree, but that is not what is seen here or in other examples (e.g. sympatric oviraptorosaur crests, tyrannosaur hornlets).

Many of the structures seen in non-avialan dinosaurs are large and presumably represented significant investments in growth, maintenance, and transport (Henderson, 1999 estimated the plates of *Stegosaurus* to be some 15% of the animal's mass). Numerous other, more 'cost-effective' ways of separating two species are apparent (i.e. the 'zero cost' signals of Knell & Sampson, 2011, such as colour or scent), any of which, or combination of which, could remove the need for the exaggerated structures seen in these taxa. As such, if we consider these structures purely within the context of the species recognition hypothesis, they are redundant and costly. These features are plastic and potentially subject to rapid evolution: we would predict that they should either have been lost, or moved towards a zero-cost signal that still benefits both parties (as suggested by Knell & Sampson, 2011; see e.g. Losos, 1985; Alatalo, Gustafsson & Lundberg, 1994).

An additional factor that should be mentioned here concerns the sheer number of exaggerated structures present in some non-avialan dinosaur taxa. If 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. Instead, however, we see numerous different signals that would surely be redundant within this context. In ceratopsians for example, we see elaboration in nasal horn, brow horn, jugal boss *and* frill midline and frill edge morphology (in additional to differences in body size, proportions, and integumentary anatomy!) when the mere presence or absence of a single horn alone would be sufficient to differentiate between sympatric species otherwise similar in size, shape, colour and behaviour. Within the context of this specific argument, note that multiple signals are known to correlate with sexual selection (Omland, 1996).

In any case, it is not clear that species recognition requires the existence of exaggerated structures at all. Among extant taxa, sympatric members of species complexes, including

tyrant flycatchers (Birdsley, 2002), bushbabies (Zimmerman, 1990), anoles (Jenssen & Gladson, 1984), frogs (Heyer, García-Lopez & Cardoso, 1996) and numerous insects (Wells & Henry, 1998) have no apparent trouble in recognizing conspecifics or potential mates, and there is no reason to think sympatric dinosaur groups would have been different (as suggested by, for example, those sympatric iguanodontians that lack the crests present in hadrosaurs).

In short, in addition to the issues of mutual sexual selection and social dominance characteristics, it seems plausible that there may be several sympatric, closely related species with exaggerated structures where those structures are too similar to be easily separated on osteological morphology alone. The benefits of such structures would thus be profoundly limited while the costs would be potentially high.

Other issues with the species recognition hypothesis

Several additional questions present problems for the species recognition hypothesis in non-avialan dinosaurs. As noted by Knell & Sampson (2011), there has yet to be any documented case in any extant species where a crest or similar structure functions primarily in species recognition. Padian & Horner (2011b) countered that species recognition has been little studied, and indeed Mendelson and Shaw (2012) noted that, to date, study has been both limited (in terms of documenting increased selection for correct identification of mates) and problematic. It is true that studies of species recognition in extant taxa are uncommon; however, some ethological studies have specifically tested the species recognition hypothesis with respect to the presence of exaggerated structures and found it wanting (e.g. Harrison & Poe, 2012). That no extant species, including the thousands of extant dinosaurs, 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. Similarly, if such structures were so important for non-avialan dinosaurs, their absence, reduction or loss in various lineages is incongruous.

Critically, it is not clear how such a structure would evolve to separate putative species through mate identification. Given that extant taxa do not appear to be using these structures for species recognition, a plausible mechanism is required to explain their origin, retention and propagation, and to our knowledge none has been proposed. If speciation occurred allopatrically, an exaggerated structure would be unnecessary (see Alatalo et al., 1994) because the populations would not be at risk of interbreeding. Ergo, such structures could only be generated during sympatric speciation events. A single interbreeding population would likely have relatively little variance in structure, size and form (be that a small crest vs. none, or two versions of a single crest). Individuals of the population might prefer one form of crest over another, or a crest over none, but this would represent mate *choice*, not mate *recognition*. We may, of course, have overlooked an obvious and simple mecha-

nism for this, but the previously hypothesized example would appear to be a problem for the species recognition hypothesis.

In addition, while individuals may prefer one potential mate over another, low ranking/low quality animals could take any mating opportunities available. The impulse to breed is generally higher in an organism than choosiness over a potential mate, as demonstrated by the mating habits and ready hybridization of numerous species (e.g. see Mendelson & Shaw, 2012). Highly distinct, wild mammal, lizard and bird taxa hybridize on occasion (sometimes on regular occasion), so even profoundly different signals (i.e. exaggerated structures – as seen for example in pheasants; Johnsgard, 1983) may not help separate two species and prevent incorrect matings. This is contra Padian & Horner (2011b) who asserted that 'an animal cannot consider mating with another unless it first recognizes that they are conspecific'. Incorrect matings can certainly be costly, although in some cases a 'wrong' mating may affect males in only a very limited manner with little penalty of investment or effort relative to females. Large and heavy structures are therefore costly signals that may not even prevent bad matings.

Rapid morphological change and species recognition

Torosaurus, *Triceratops* and *Nedoceratops* are contemporaneous ceratopsids from the Late Cretaceous of western North America. Although conventionally regarded as distinct (albeit closely related) taxa, all have been regarded as growth forms of the same taxon by some authors (Scannella & Horner, 2010). These authors used data from skull shape, skull bone surface texture and frill bone histology to argue that members of this lineage underwent major morphological shifts during ontogeny, with '*Triceratops*' morphing into '*Torosaurus*' via '*Nedoceratops*' (similar transitions have been hypothesized for some pachycephalosaurs). Other authors dispute this proposed ontogenetic morphing (Farke, 2011; Longrich & Field, 2012). The ontogenetic morphing hypothesis is relevant here in that each putative morph is anatomically distinct in terms of cranial morphology. According to Padian & Horner (2011b), each putative morph demonstrates 'status recognition within these species, because they show the social status of individuals at various ontogenetic stages'; mate recognition is thus integral to this interpretation.

However, the presence of medullary bone in some immature Mesozoic dinosaur specimens shows that members of at least some species could reproduce before reaching skeletal maturity (e.g. Lee & Werning, 2008). If exaggerated cranial structures exist to provide a clear and unambiguous signal of ontogenetic status, then this hypothesized transition from one morph to another implies the very opposite of a clear and unambiguous signal. Individuals may encounter a viable mate with any one of the three frill and horn morphologies present, or some intermediate form between them. Correctly identifying a conspecific of the correct status (social or reproductive) gets harder, not easier, when several transforming morphs are present. Intraspecific variation is also

present, and Scannella & Horner (2010) noted that horn core form was still being remodelled in their hypothesized 'adult' *Torosaurus* specimens. This would also affect herd coherency in the same way, with confusing signals being broadcast as to the identity of the individual.

However, a specific identity for different age or social classes of animal could support a social dominance hypothesis. Non-adult animals that either herd or control territories would presumably be required to fend off rivals and provide a relatively clear signal as to their age or social position, but this would represent neither herd coherency nor mate recognition.

Rapid crest growth late in ontogeny was also used by Padian & Horner (2011*a*) as evidence for the functioning of crests in species recognition. However, this contradicts the herd coherency model: gregarious behaviour is well established for juvenile dinosaurs across several lineages (Varricchio, 2011), yet these lacked exaggerated structures as juveniles, and also as adults in some cases. In the case of *Triceratops*, juveniles with small crests and horns may have been gregarious, while adults bearing huge frills and horns were potentially solitary (Mathews *et al.*, 2009). Moreover, late ontogenetic development is also seen in sexually selected structures, or indeed in any structure used by adults but not juveniles (e.g. Caro *et al.*, 2003; Knell *et al.*, 2012): this line of evidence is thus equivocal at best.

Conclusions

We conclude that the species recognition hypothesis lacks support in non-avialan dinosaurs. There is currently no evidence that in extant taxa, exaggerated structures have evolved primarily through species recognition. We suggest that allopatric speciation would make the use of exaggerated structures irrelevant in the context of species recognition and that sympatric speciation would not lead to separation except through mate choice.

At least some taxa could not have benefited from the existence of these structures because they would provide no obvious benefit in terms of recognition by conspecifics, but would represent an active penalty in terms of growth and maintenance. Many unadorned juvenile animals seem to have been gregarious while adults perhaps were not: a situation that argues against a herd coherency role for these structures and against the idea that late ontogenetic development of such structures supports a species recognition role over a sexual selection one. The extreme ontogenetic change hypothesized to occur in ceratopsians and other dinosaurs is controversial and requires further research: if valid, however, it appears incompatible with the hypothesized role of exaggerated structures in species recognition, because changes in the shape of such structures would confuse, not assist, the identification of potential mates and herd members.

The idea that random evolution of exaggerated structures supports the species recognition hypothesis is not supported. Nor is the argument that the species recognition hypothesis is supported by the existence of such structures in locales where numerous closely related species occurred in sympatry. Future analyses must first establish which, if any, factors may correlate with 'species recognition' in extant clades before testing for them.

We cannot rule out species recognition as a hypothesis: perhaps some non-avialan dinosaurs did rely on these structures to help identify one another, and perhaps species recognition was indeed the primary mechanism driving the evolution and retention of these structures. However, there is currently no good evidence that might support this hypothesis and it should not currently be considered viable.

Acknowledgements

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