Does mutual sexual selection explain the evolution of head crests in pterosaurs and dinosaurs?

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Cranial ornamentation is widespread throughout the extinct non-avialan Ornithodira, being present throughout Pterosauria, Ornithischia and Saurischia. Ornaments take many forms, and can be composed of at least a dozen different skull bones, indicating multiple origins. Many of these crests serve no clear survival function and it has been suggested that their primary use was for species recognition or sexual display. The distribution within Ornithodira and the form and position of these crests suggest sexual selection as a key factor, although the role of the latter has often been rejected on the grounds of an apparent lack of sexual dimorphism in many species. Surprisingly, the phenomenon of mutual sexual selection – where both males and females are ornamented and both select mates – has been ignored in research on fossil ornithodirans, despite a rich history of research and frequent expression in modern birds. Here, we review the available evidence for the functions of ornithodiran cranial crests and conclude that mutual sexual selection presents a valid hypothesis for their presence and distribution. The integration of mutual sexual selection into future studies is critical to our understanding of ornithodiran ecology, evolution and particularly questions regarding sexual dimorphism. □ *Behaviour, Dinosauria, ornaments, Pterosauria, sexual selection.*

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Ornithodira is a node-based archosaurian clade that incorporates *Scleromochlus*, Pterosauria, Dinosauria and all descendants of their most recent common ancestor (Sereno 1991). Ornithodira therefore includes all bird-branch archosaurs and excludes crocodile-branch archosaurs (see Fig. 1). In the present article we are interested in discussing the possibility of sexual selection in non-avialan ornithodirans and mostly ignore birds. Fossil ornithodirans likely had excellent colour vision (Jacobs & Rowe 2004; Stevens 2006) in common with their extant representatives and the ancestral vertebrate condition (Yokoyama 2002). Many are also considered gregarious based on bonebeds and trackway evidence (Unwin 2005; Lockley *et al.* 2008; Isles 2010), and such aspects of behaviour as nesting, post-hatching parental care, ritualized intraspecific combat, vocal signalling and co-operative hunting have all been inferred for fossil ornithodiran species.

The term 'cranial crest' can be used for several different structures (typically, but not necessarily, osteological). Sagittal crests that form the anchor points for large jaw musculature are widely present in disparate vertebrate lineages. Such crests need not play a direct role in intraspecific display, although, if crest size is correlated with the size of the attached muscles and in turn with bite strength, crest size could provide an indication of fitness (e.g. Measey *et al.* 2009 on living chameleons). This would open the crest to exaggeration, by sexual selection, beyond the design optimal for jaw mechanics alone. For the purposes of this article, we exclude bony crests whose primary function was apparently to form the anchor point for musculature. However, whether some structures seen in fossil taxa evolved for utilitarian reasons unrelated to signalling or not remains difficult to establish given that any given ornament may have one or a number of secondary functions, potentially, including thermoregulation, manipulation of the environment and defence against predators. An example is provided by the keratin-sheathed casques of cassowaries which, whilst sexually dimorphic and apparently employed in display, may also be used to move debris on the forest floor (Folch 1992), as foliage deflectors, and as aids to detecting infrasonic calls (Mack & Jones 2003). We must therefore be cautious when making statements about the
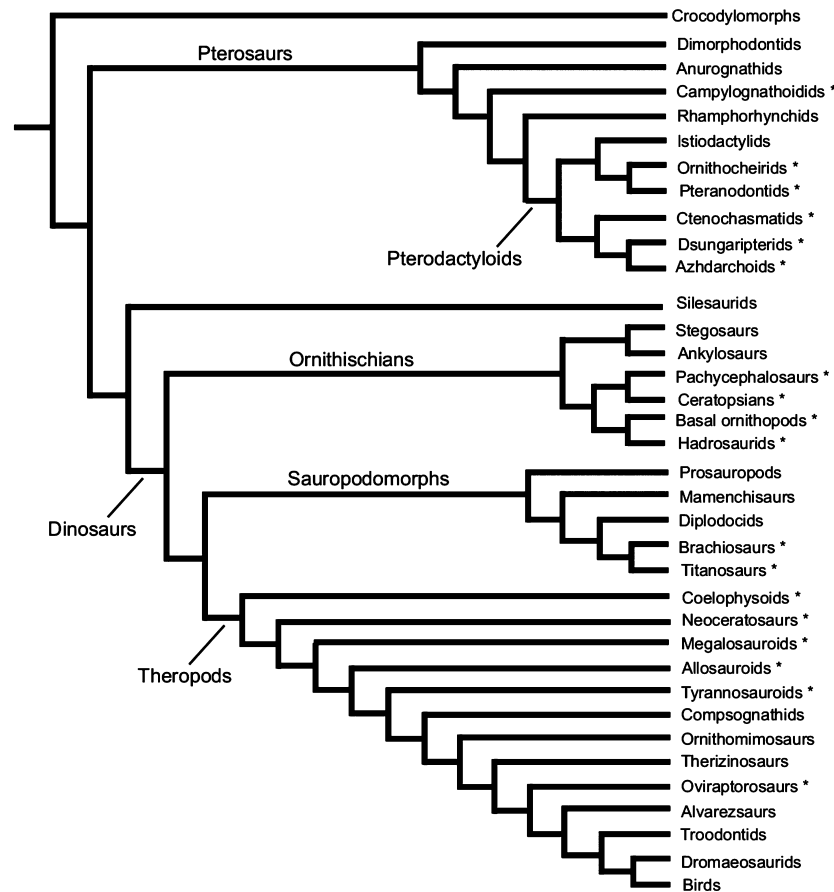
Fig. 1. A phylogeny of Ornithodira showing most major clades: those in which at least some taxa possess cranial crests are indicated with an asterisk. The tree combines data from Unwin (2003, 2005) and Lloyd *et al.* (2008).

use and function of a given cranial crest; however, well-reasoned hypotheses can be proposed or rejected in the light of biomechanical analyses and comparison with extant analogues.

While this article deals exclusively with cranial ornaments, note that various dinosaurs exhibit additional morphological features that may well have served similar purposes. The plates of *Stegosaurus*, as just one example, have been suggested to have had a wide variety of functions (e.g. defence, thermoregulation, species recognition), among which are visual display (Main *et al.* 2000).

Specific cases of sexual dimorphism and selection are difficult to confirm in fossil taxa, especially given that sample sizes are typically small. The latter point makes it difficult to distinguish sexual dimorphism from inter- or intraspecific identification. However, a role in sexual selection can often be strongly inferred for many of the relevant structures: the cranial crests of the theropod *Dilophosaurus*, for example, were fragile and in a position unlikely to have been useful for a function in predation (e.g. in anchoring jaw muscles, or reinforcing the skull from impact). It seems most

plausible that they were used for display, most likely either sexual or social. An alternative signalling function for such crests, that of a warning (aposematic) display directed at predators, will be discussed later.

We provide here a brief review of the better known ornamented non-avialian ornithodirans and of the interpretations put forward to explain their cranial crests. These involve their possible function as sexual signals (Galton 1971), as general intra or interspecific signalling devices (see Hopson 1975), for species recognition (Hopson 1975), as mechanical structures to assist feeding or locomotion (Stein 1975), for thermoregulation (Wheeler 1978), or as intra- or interspecific weapons or defensive organs (Colbert 1948; Sampson 1995). Some lineages are notable for the number of hypotheses proposed to explain the origin or function of their crests (notably ceratopsians), while others (e.g. oviraptorosaurs) have been somewhat neglected. We argue that, while some or even many of these structures may have had a secondary role, their primary function was of signalling to conspecifics for sexual display or dominance. Furthermore, we contend that mutual sexual selection (where sexual

selection, via any proposed mechanisms, acts in both sexes) was potentially rife within fossil Ornithodira. In taxa such as the ceratopsian *Pachyrhinosaurus*, we know of large numbers of specimens (e.g. 15 adults found in a single locality), all of which are crested; what has been interpreted as dimorphism indicates that both sexes are represented, so both males and females were ornamented with crests (Sampson 1995).

Sexual selection and mutual sexual selection

Sexual selection was invoked by Darwin (1871) to explain the widespread occurrence of costly, often sexually dimorphic, traits that appeared to have no role in promoting survival or nurturing of the young (Andersson 1994). Instead, Darwin proposed that such traits aid the bearer in reproductive competition, either in combat and other forms of same-sex rivalry (intrasexual selection), or through influencing the opposite sex's mating decisions (intersexual selection). Because he framed his theory of natural selection in terms of survival advantage, and because intersexual selection often favours extravagant ornaments and costly displays, Darwin (and most subsequent authors) viewed sexual selection as acting in opposition to natural, 'viability', selection (Cronin 1991; Andersson 1994).

Sexual selection has at times been disregarded as a possible evolutionary cause of ornaments in some species, simply because all specimens (and therefore presumably both males and females) are ornamented (Hopson 1975) or because clear sexual dimorphism is absent (Padian & Horner 2011a). However, in extant species including birds, it is common for partial expression of 'male' ornamentation to be present in both sexes (Amundsen 2000; Kraaijeveld *et al.* 2007), and clear bimodal distributions are inevitably hard to detect in fossil taxa without large sample sizes. Furthermore, while sexual dimorphism is often an expected product of sexual selection (due to sexual differences in the costs and benefits of parental investment or mate competition (Trivers 1972; Andersson 1994)), it is by no means inevitable.

The theory of mutual sexual selection has a long history, going back to Huxley (1914) at least, and in recent years has attracted renewed interest in behavioural ecology (Kraaijeveld *et al.* 2007). It has, in part, been stimulated by empirical demonstrations of mutual mate choice based on the same ornaments (e.g. Jones & Hunter 1993, 1999; Hunt *et al.* 1999; Kraaijeveld *et al.* 2004; Komdeur *et al.* 2005), a realization that female ornamentation has, historically, been overlooked (Amundsen 2000), and an interest

among theoreticians in establishing the conditions under which mutual mate choice might be expected (Johnstone *et al.* 1996; Johnstone 1997; Kokko and Johnstone 2002). Models such as the latter indicate that mutual sexual selection is more likely when both sexes show high variation in individual quality. This variation need not be genetic, for example where a partner can offer high direct (non-genetic) benefits, such as parental care. Kokko & Johnstone (2002) showed that mutual mate choice is particularly expected when both parents contribute to care in a synergistic fashion. An instructive example is the crested auklet, *Aethia cristatella*, a monogamous seabird with biparental care, in which both sexes bear feather plumes on their heads, both sexes prefer mates with longer crests, and longer crested individuals are dominant within each sex (Jones & Hunter 1993, 1999; Fig. 2). The fact that an ornament can function in both intra- and intersexual selection is not surprising if the development of the ornament is condition dependent (Berglund *et al.* 1996).

The variance in quality of potential mates of each sex is, of course, unknown in Mesozoic ornithodirans. It has recently been argued that males may have played a substantive parental role in some non-avialian theropod taxa (Varricchio *et al.* 2008) but the evidence marshalled to support this hypothesis is far from convincing (Isles 2010). Note that a large amount of research now shows that sexual dimorphism is not a requirement for sexual selection to be hypothesized as the primary process acting on a given trait.

Birds are historically the clade in which sexual selection (mutual or otherwise) has been documented most frequently. However, this is at least in part due to their convenience for research (small, diurnal animals with clear visual signals) rather than mutual sexual selection being unusually common in the group, and numerous examples of mutual sexual selection have since been documented elsewhere (Prudic *et al.* 2011). Nevertheless, they support the concepts laid out here for extinct non-avialian ornithodirans since birds form part of the extant phylogenetic bracket for Mesozoic ornithodirans and clearly have close evolutionary ties with fossil members of the clade. The recent discovery of long, apparently ornamental, integumentary tail structures in a non-avialian theropod (Zhang *et al.* 2008) reinforces the expectation that patterns of sexual selection present in birds are indeed reflected in Mesozoic ornithodirans – however, mutual sexual selection has not, to our knowledge, even been suggested as a possible factor in the origin or evolution of fossil ornithodiran crests and has only even been mentioned in passing in two previous papers (Taylor *et al.* 2011; Tomkins *et al.* 2010).
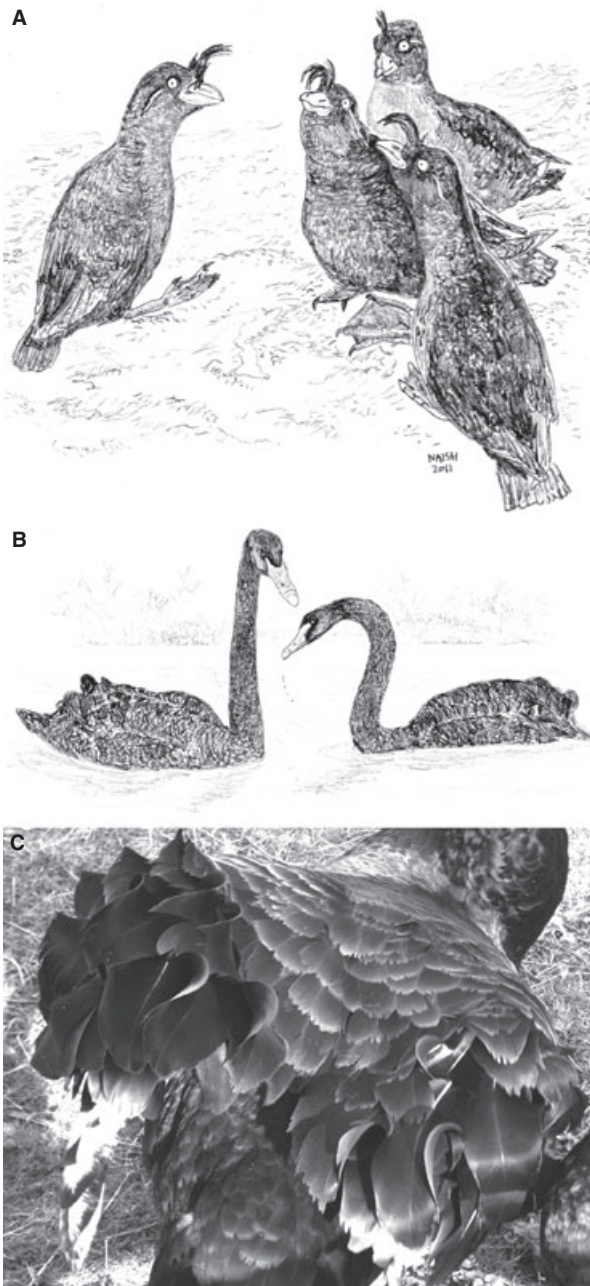
Fig. 3. Cranial crests in pterosaurs. Top: the ornithocheiroid *Ornithocheirus* with crests on both the upper and lower jaws at the tip of the rostrum. Middle, the dsungaripterid *Dsungaripterus* with both a dorsal crest providing the anchor point for a soft tissue extension and a small, posteriorly positioned rod. Bottom, the pteranodontid *Pteranodon* with a dorsal crest. Images in left lateral view and not to scale and based on Unwin (2003, 2005).

Pterosauria

Cranial crests of a wide diversity are present in almost every pterosaurian clade (Wellnhofer 1991; Unwin 2005; Martill & Naish 2006). Furthermore, the recent discovery that even non-pterodactyloid taxa possess soft tissue crests (Czerkas & Ji 2002) raises the possibility that members of nearly all 'family level' pterosaur clades were crested to some degree (the unusual anurognathids remain the only likely exception). Crests formed exclusively along the sagittal plane of the skull include those limited to the anterior (e.g. *Ornithocheirus*), posterior (e.g. *Pteranodon*) or full length of the skull (e.g. *Dsungaripterus*) (Fig. 3).

The majority of pterosaur taxa are known from single specimens (Unwin 2005) and as a result it cannot generally be determined if crests were present in both sexes. However, sexual dimorphism has been inferred in *Pteranodon* (Bennett 1992, 1994) and suggested in a number of other taxa (Bennett 1995; and references therein; Unwin 2005) and most notably in *Darwinopterus*, where a skeletally mature, crestless individual (identical in size to conspecific crested individuals) is preserved in association with an indisputable egg (Lü *et al.* 2011). Adolescent development of a bony crest has been proposed for thalassodromids (Martill & Naish 2006) and *Pteranodon* shows strong allometric growth of the crest (Tomkins *et al.* 2010), suggesting a role that only becomes relevant after maturity. This is

Fig. 2. Mutual sexual selection as practiced by extant members of Ornithodira. A, crested auklet *Aethia cristatella* (illustration based on photo in Gaston & Jones (1998)): both males and females use their forehead crests in sexual display. B, black swan *Cygnus atratus*: both males and females use their curled wing feathers in social and sexual display. C, close-up photo showing curled wing feathers present in both male and female black swan. Photo by D. W. E. Hone.

Taxonomic review

In this section, we deal with the presence of various crests and ornaments and the hypotheses proposed to explain their presence; the details of their purported functions are discussed later.
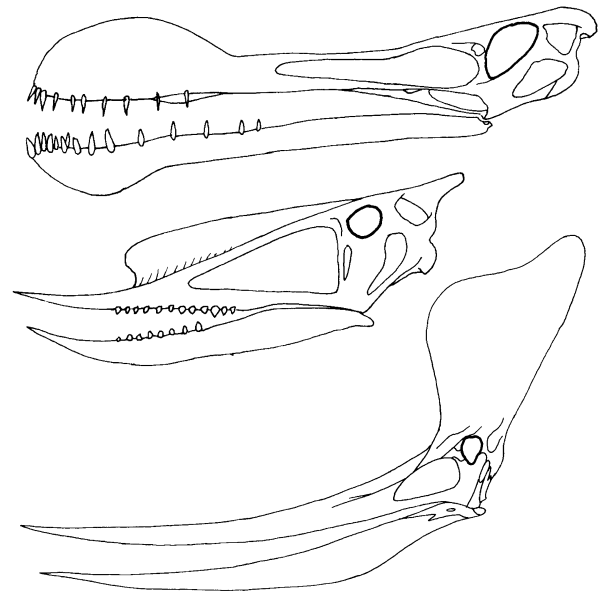
significant as pterosaurs were likely precocial and capable of flight shortly after hatching (Bennett 1995; Unwin 2005). Although not definitive evidence, the coincident appearance of a structure with maturity is a hallmark of a role in sexual selection. Numerous hypotheses have been proposed to account for the evolution of these crests, including use in sexual display, steering in flight, and thermoregulation.

Ornithischian dinosaurs

Among the best-known crested dinosaurs are the lambeosaurine hadrosaurs of Campanian–Maastrichtian Asia and western North America. Their cranial crests include sagittally oriented plate-like and fan-like structures as well as posteriorly projecting tubes. Previously suggested roles as air tanks or snorkels used in aquatic feeding, or as hypertrophied olfactory chambers, are not supported and it is generally agreed that their morphology and diversity makes a sexual display function the most likely one.

As with ceratopsians (see below), osteological sexual dimorphism appears limited, with both sexes apparently being equally ornamented (Horner *et al.* 2004) where large sample sizes permit inference (*n* = tens of animals in some cases: Dodson *et al.* 2004). Ideas on the degree of sexual dimorphism present in lambeosaurines have changed in recent years. Traditionally, different crest morphologies among otherwise similar individuals were regarded as indicators of specific status, resulting in a taxonomic regime where numerous similar species were named within a genus. However, Dodson (1975) and Hopson (1975) argued that specimens named as representing distinct 'species' were, more likely, different ontogenetic stages and/or sexes of the same species. Consequently, the presence of marked sexual dimorphism in cranial crest morphology became popular to the extent that, for example, the hook-crested *Parasaurolophus cyrtocristatus* was imagined as the 'female' to the 'male' tube-crested *P. walkeri* (Hopson 1975). These notions of intraspecific variation may hold true for some lambeosaurine taxa. However, in others – such as the *Parasaurolophus* species – these 'sexes' are neither contemporaneous nor found in close geographical proximity and they differ in such details as internal crest architecture (Sullivan & Williamson 1999; Gates *et al.* 2007) indicating that they are indeed distinct taxa.

Two predominantly Cretaceous ornithischian clades, Pachycephalosauria and Ceratopsia, are united within Marginocephalia in part because they share a bony shelf at the back of the skull (Sereno 1986): cranial ornamentation may thus have evolved at the base of this group. Basal ceratopsians (psittacosaurids and non-ceratopsid neoceratopsians) exhibit laterally projecting subtriangular bosses on their jugals. Jugal bosses are also present in heterodontosaurids, an archaic ornithischian clade of controversial phylogenetic position (e.g. Norman *et al.* 2004). A functional interpretation has yet to be proposed for these structures: they may conceivably have played an anti-predator role, but it is also plausible that they played a role in sexual combat and competition.

Among ceratopsians, neoceratopsians combine a bony frill with supraorbital and/or nasal horns, jugal bosses and/or spines around the frill margins (Dodson *et al.* 2004; see Fig. 4). Makovicky & Norell (2006) argued that the uniform morphology of the frill in basal ceratopsians suggest an origin through natural (viability) selection, and a later display role as an exaptation. Sexual dimorphism has long been inferred for members of Neoceratopsia (e.g. Brown & Schlaikjer 1940; Dodson 1976, 1990; Lehman 1990), but it is notable that, again, all individuals exhibit cranial ornamentation and that the proposed degree of sexual dimorphism is weak.

The unusual thick-roofed skulls of pachycephalosaurs (see Fig. 4) have long been interpreted as functioning in intraspecific fighting or combat with predators (Colbert 1955; Galton 1970). Skull dome surface texture shows that a thick keratinous covering, presumably employed in display, was present. Even assuming a role in fighting, a display function is still supported by the presence of diverse bosses and spikes. In the Late Cretaceous taxa *Stygimoloch* and *Dracorex*, for example (though, see Horner & Goodwin 2009), clusters of elongate horns were located along the rear margin of the skull (Carpenter 1997; Goodwin *et al.* 1998; Bakker *et al.* 2006); in the live animal, these would presumably only be apparent when the head was dipped towards the ground in display and would have been difficult to bring to bear on an antagonist. Sexual dimorphism has also been claimed for pachycephalosaurs, notably *Stegoceras* (Chapman *et al.* 1997; though, see Sullivan 2003).

Saurischian dinosaurs

Diverse cranial crests were present among non-avialian theropods (Fig. 5). In Triassic and Lower Jurassic theropods, coelophysoids and their close relatives are well known for exhibiting paired crests on the dorsal surface of the snout: in *Dilophosaurus wetherilli* the crests are laterally thin, semi-circular, and with short, posteriorly projecting spikes (Welles 1984), while in the remarkable *Cryolophosaurus* an anteriorly facing, comb-like crest rises from the supraorbital region (Smith *et al.* 2007).

Various theropod lineages exhibit crests and horns. Neoceratosaurs are well known for the narial and
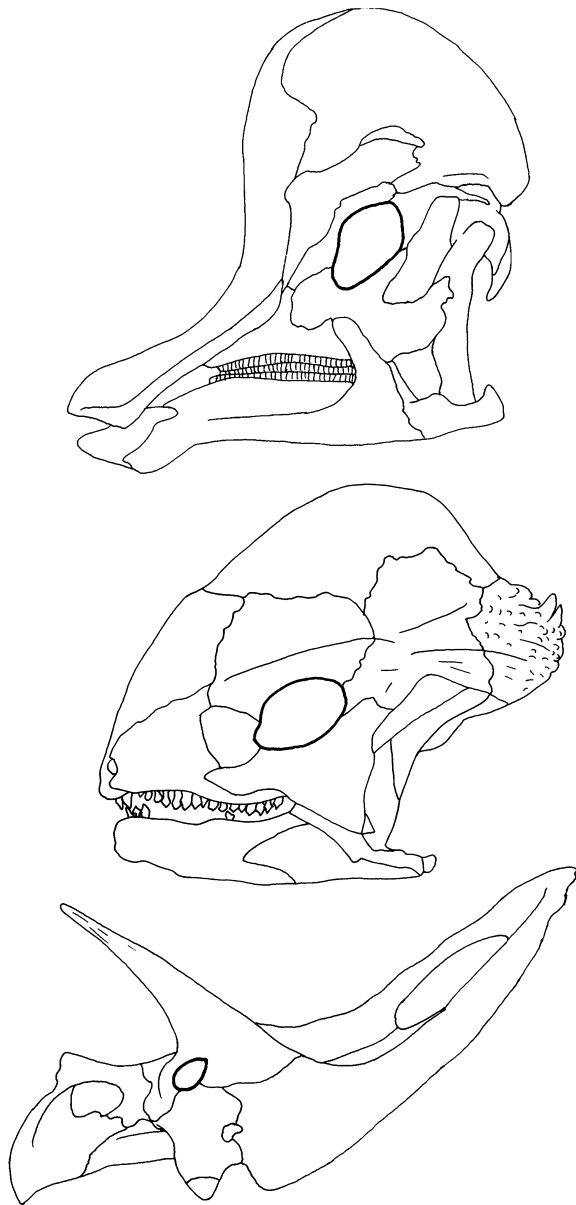
Fig. 4. Cranial crests in ornithischian dinosaurs in left lateral view. Top, the hadrosaur *Corythosaurus* with a laterally compressed, plate-shaped crest. Middle, the cranial crest of the pachycephalosaur *Stegoceras* with the dome of solid bone on the top of the head. Bottom, the neoceratopsian *Torosaurus* with a large posterior frill, large brow horns and a small nasal horn. Images in left lateral view and not to scale and based on Norman (1991) and Romer (1956).

Fig. 5. Cranial crests in theropod dinosaurs. Top, the ceratosaur *Ceratosaurus* with a large nasal horn. Middle, the basal tetanuran *Monolophosaurus* with a hollow crest projecting dorsally from much of the length of the skull. Bottom, the basal theropod *Dilophosaurus* with thin paired plates of bone on the skull. Images in left lateral view and not to scale, modified from Tykoski & Rowe (2004) and Holtz *et al.* (2004).

supraorbital horns of *Ceratosaurus* (Fig. 5) and the supraorbital horns of abelisaurids such as *Carnotaurus sastrei*. Megalosauroids and allosauroids include taxa that possess supraorbital horns, post-orbital hornlets and twin parallel ridges along the dorsal surface of the snout. In *Monolophosaurus jiangi* an elongate, hollow, subrectangular crest extends for the entire snout length (Zhao & Currie 1993, fig. 5). Notably, coelurosaurs were modest in their development of cranial ornamentation. Rugose, mid-line snout ridges were
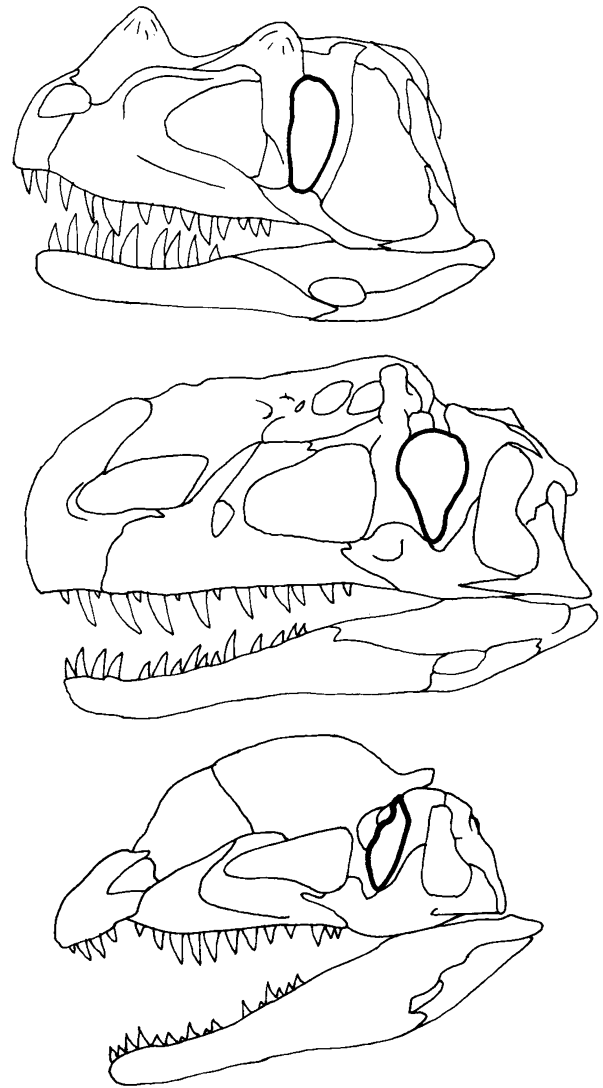
present in some tyrannosauroids and ornithomimosaurs (Paul 1988), the tyrannosauroid *Guanlong wucaii* exhibits a bizarre, laterally compressed crest (Xu *et al.* 2006), while others possess pre-orbital and post-orbital hornlets and bosses. A soft tissue crest has been reported for the ornithomimosaur *Pelecanimimus polyodon* (Pérez-Moreno *et al.* 1994) but the suggested presence of bony horns or spikes in *Garudimimus brevipes* has proved erroneous (Kobayashi & Barsbold 2005).

Among maniraptorans, oviraptorosaurs are well known for their casque-like crests and appear unique among non-avialian maniraptorans in this respect:

non-avialian maniraptorans are otherwise notable for their lack of cranial ornamentation. The large numbers of Mesozoic maniraptoran taxa now known (many of which are represented by several, well preserved, specimens that include soft tissue preservation) allows us to state with confidence that crests are indeed mostly absent in the Mesozoic members of this clade and that this is not an artefact of preservation or any other factor.

A small number of sauropods exhibit unusual cranial features which could have acted as sexual signals. The raised internarial bars of taxa such as *Giraffatitan brancai* and *Europasaurus holgeri* may have had an as yet undetermined utilitarian purpose, but could equally be considered signalling structures.

Functional review

Since bony cranial crests would have had significant developmental costs, and energetic costs of transport and maintenance, we reject the possibility that crests had no adaptive function or were under neutral selection. Obviously, discussing the morphology and likely function of every cranial crest in every fossil ornithodiran is beyond the scope of this paper. However, it is worth discussing in more detail some of the more common interpretations that have been posited for certain taxa (Table 1) as well as those interpretations that contradict the data. In a number of cases, explicit tests of crest functional morphology have been undertaken. Only by elucidating and rejecting or accepting the validity of a given hypothesis for a crest function can we work towards an understanding of their use.

While juvenile dinosaurs and pterosaurs are rare, in those crested taxa or clades for which juveniles are known, the juveniles either lack crests, or possess only incipient versions (e.g. Sampson 1995; Forster 1997; Martill & Naish 2006; Farke 2011). It seems that crests grew allometrically during ontogeny and only reached their full-size or final adult form late in development (Goodwin *et al.* 2006; Horner & Goodwin 2006; Farke 2011). That they were not needed by juvenile animals suggests that they would have been costly prior to adulthood, in turn suggesting a sexually selected function. Tomkins *et al.* (2010) explicitly suggested that high degrees of positive allometry indicate roles in sexual display rather than in 'functional' roles such as thermoregulation, though it should be noted that positive allometry is not necessarily a definitive characteristic of sexual selection (Bonduriansky 2007).

Thermoregulation

Many ornithodiran crests appear poorly suited to function effectively as thermoregulatory structures and lack the features present in morphological structures inferred elsewhere to have had a thermoregulatory role (such as the dorsal sails of edaphosaurid and sphenacodontid synapsids: see Bramwell & Fellgett 1973).

While large when compared to the size of the skull in cases, few ornithodiran crests were large enough to have significantly increased the surface area of the animal concerned, even if soft tissue extensions are included. Behavioural adaptations would be far more effective and, if an animal regularly required the use of extra surfaces to regulate temperature, it seems more likely that physiological or structural solutions other than a robust bony cranial crest would have evolved.

The bony crests of several azhdarchoid pterosaurs, most notably *Thalassodromeus sethi*, possess grooved surfaces that almost certainly represent blood vessel channels, and it has been suggested that this pattern of vasculature might indicate a thermoregulatory function (Kellner & Campos 2002). However, it is more likely that this represents the sort of vasculature typically associated with the nourishment of growing tissues. This argument is doubly applicable to maritime pterosaurs where cooling wind and water would be available in times of high temperatures; furthermore, the large wings (with their extensive vasculature and

Table 1. Major hypotheses of ornithodiran cranial crest function. Here, we only include common or strongly argued cases from the literature and do not feature 'one offs' like the snorkel hypothesis for some hadrosaur crests. For simplicity, the taxonomic groupings are based primarily on how the hypotheses have been framed in the literature. These may therefore be perfectly applicable to other taxa not mentioned here or were originally only posited for a single taxon.

	Thermoregulation	Interspecific combat	Defence	Warning signals	Intraspecific combat	Species recognition	Non-sexual signals	Other biomechanical function
Pterodactyloid Pterosaurs	X					X		X
Hadrosaurs				X		X	X	
Pachycephalosaurs		X	X		X	X		
Ceratopsians	X	X	X	X	X	X	X	
Theropods		X			X		X	

air-sac system: see Frey *et al.* 2003) could have collected or dissipated far more heat than a laterally facing crest. Furthermore, the patterns of vasculature seen on the skulls of *Thalassodromeus* and other pterosaurs are comparable in size and extent to those present on, for example, the premaxillary bones of some birds (D. Naish, personal observations). In other words, the inferred thermoregulatory vessel pattern probably represents the normal amount of vasculature present where keratinous structures grow over bones, and not specialization for thermoregulation.

A minority of crested ornithodirans may have used their crest for thermoregulation, notably those neoceratopsians (Fig. 4) in which the crests were very large compared to the size of the body. However, the evidence for substantial ontogenetic variation in these structures and wide degree of variation seen among closely related members of the group (including in taxa recovered from the same fossil localities) argues against this. It can be predicted that specialized thermoregulatory structures should be found in organisms at risk from severe temperature changes, particularly in relatively small animals susceptible to cold or heat stress, or in animals that inhabit extreme environments. In contrast, cranial crests are present across a wide variety of phylogenetically diverse ornithodirans that span a substantial range in body size and occurred in often equable environments. The substantial metabolic investment incurred in growing and maintaining cranial crests strongly indicates that any thermoregulatory role was minor and facultative, as it is in the horns of extant bovids (Taylor 1960; Hoefs 2000).

Interspecific combat

It is likely that at least some crests functioned as weapons used against predators and interspecific competitors, most notably the large horns of many neoceratopsians (Dodson & Currie 1990). Certainly one *Triceratops* specimen has healed tooth marks from a *Tyrannosaurus* on one of its brow horns, suggesting that it quite literally came face-to-face with a predator and survived (Happ 2008). It is perhaps likely that these animals engaged predators or other aggressors with their horns as a relatively common part of their behaviour. If horns were primarily used for attacking or threatening predators it raises the question as to why members of some neoceratopsian lineages apparently reduced or lost their horns. Regardless of their use, it has been noted that these horns did not likely evolve for anti-predator functions (Dodson 1976; Spassov 1979; Sampson 2001; Dodson *et al.* 2004; Farke *et al.* 2009): notably, early ceratopsians lack horns but do possess neck frills.

Turning to pachycephalosaurs, the first line of defence among these obligate bipeds was almost certainly escape rather than attack, as directly challenging a predator is typically limited to large herbivores similar in size or bigger and slower then their potential predator. However, with no other option, it is likely that a pachycephalosaur would engage in combat, though whether or not the skull and body were capable of absorbing the shock of such an attack is uncertain (Carpenter 1997; Goodwin & Horner 2004; Snively & Cox 2008).

Defence

It has been suggested that neoceratopsians used their frills as defensive organs against predators (Colbert 1948). Views differ as to how well frills may have performed when placed under such stress as the bite of a tyrannosaurid. Farke *et al.* (2010) used finite element analysis to examine the ability of the *Triceratops* frill to withstand loading, and identified features consistent with resistance to assault. However, tooth-marked bones and estimated bite strengths both show that tyrannosaurids were certainly capable of biting into or through thicker pieces of bone than the neck frills of ceratopsians (Erickson *et al.* 1996), rendering it doubtful that the frills were specialized, anti-theropod defensive structures.

The epoccipitals of some neoceratopsians create a serrated border to the frill. Combined with the mobility of the frill as part of the skull, this implies a possible role in deterring predation. However, this defence would only be effective when the neoceratopsian had reached large size and had developed the full adult complement of spikes and other structures. In basal taxa with small frills and no spikes, this would not have been effective: while the frill may therefore have served as a defensive structure or been used in threat displays, it is again unlikely that this was its original purpose, since it evidently originated at small size. In any case, it is perhaps unlikely that large theropods would attack dangerous animals like adult ceratopsians when other, more vulnerable prey (namely juveniles) were available (Hone & Rauhut 2010).

Warning signals

The catch-all term 'warning signal' covers a diversity of strategies, with different evolutionary origins and behavioural roles (all of the following are discussed by Ruxton *et al.* 2004). Classic aposematic signals are permanently displayed, honest indicators of toxicity, unpalatability or, more generally (and accurately), unprofitability. Conversely, other signals, more accurately described as having a startle function, are

displayed suddenly and act to confuse or distract the predator, or cause it to pause long enough for the prey to escape. Other signals are facultative responses to threat and act not to startle but – as with permanently displayed aposematic signals – indicate the deleterious consequences of attacking a well-defended animal, either by indicating an ability to fight, or by falsely exaggerating body size. Most classic aposematic prey use permanently displayed colours. Because few extant aposematic species require cranial crests to advertize their unprofitable qualities, we regard it as unlikely that ornithodiran cranial crests evolved under selection for an aposematic function.

Aside from a permanent display of unprofitability, a number of ornithodiran crests have been suggested to act as facultative threat signals to potential predators or interspecific competitors in much the same way as the hood of a cobra (e.g. Farlow & Dodson 1975). However, many crests (such as those seen in theropods) are clearly too small to significantly increase the apparent size of the animal, or are present in taxa that already exhibit superior anti-predator defences (e.g. volancy in pterosaurs). Facultative displays such as those involving a sudden increase in size, or those that reveal a previously hidden bright colour, are not functions consistent with small, immobile bony crests.

Plausible exceptions to this are, once again, neoceratopsians, many of which had large neck frills that would be raised (and so 'flashed') if the head was suddenly tilted forwards and down. However, while a frill might make little difference to the intimidatory value of a group of horned ceratopsians, individual ceratopsians evidently faced conspecifics in face-to-face combat. Any function of the frill involving intraspecific intimidation would of course be tied to dominance displays and, by extension, sexual selection; we propose that a frill unambiguously signalling a willingness to charge could be co-opted for anti-predatory function. It thus seems unlikely that many, if any, fossil ornithodirans retained their crests purely for use in threat displays.

Intraspecific combat

Ceratopsians and pachycephalosaurs in particular have been imagined to engage in ritualistic, cranial-based combat (as opposed to body blows, biting etc.) (e.g. Farlow & Dodson 1975; Sampson 1995). The hypothesis of intraspecific combat in pachycephalosaurs is controversial, with studies both in favour (e.g. Snively & Cox 2008) and against (e.g. Carpenter 1997; Goodwin & Horner 2004) the idea. The long brow horns of ceratopsids were well suited for intraspecific combat and direct evidence is preserved in *Triceratops*

at least (Farke 2004; Farke *et al.* 2009). As such it seems clear that in at least some taxa, the horns and crests played a significant role in combat.

Species recognition

It is important to recognize that species recognition can sometimes be considered a subset, or even epiphenomenon, of inter-sexual selection (Ptacek 2000; and references therein). Mating with a member of the wrong species is just an extreme example of 'bad' mating, so ornaments that evolved for mate choice through sexual selection would necessarily result in divergence in mating signals between species (Littlejohn 1999). There remain examples of signals that do not serve to discriminate between potential mates within a species, but function to discriminate against heterospecifics (Ptacek 2000). Furthermore, there are reasons unassociated with sex to associate with conspecifics, so it is important to consider whether ornithodiran crests could have evolved for such reasons. It has been proposed that the crests present in closely related, morphologically similar members of some groups might aid in species recognition, either to prevent hybridization (Mayr 1970), or for maintaining herd coherency (e.g. Hopson 1975; Kellner & Campos 2002; Padian & Horner 2011a). Neither proposal stands up well to scrutiny, however, not least though a lack of support for species recognition as a driving force in any exaggerated ornament (Knell & Sampson 2011); Padian & Horner (2011b) argued that a lack of testing for the species recognition hypothesis has hindered its acceptance in extant species, but the substantial work that has been published on sexually selected ornaments is better consistent with functions in intraspecific mate competion (e.g. Andersson 1994; Berglund *et al.* 1996), as argued here.

Indeed, in the case of mate identification, the hypothesis that an animal would grow a large, unwieldy, costly crest simply to be identifiable to conspecifics seems unlikely: cranial structures are not employed this way in sympatric extant crested vertebrates species assemblages (e.g. sympatric African antelope, crested auks, phasianid gamebirds). Species recognize conspecifics by differences in colour, pattern, shape, size, acoustic or olfactory signals, and behaviour. Modern African antelope species have no difficulty identifying sympatric conspecifics despite minor differences in morphology, colouration and behaviour, while tyrant flycatchers notorious for showing little to no morphological variation exhibit clear boundaries between species, despite sympatry (e.g. Birdsley 2002). While evolution does not, of course, apparently proceed by the most efficient or appropriate route, crests have evolved many times in

many ornithodiran lineages and it seems implausible that so many highly varied crests would be required simply for conspecific recognition: indeed, a proposed role in conspecific recognition is illogical for many of the taxa concerned given that they simply do not overlap in time and space (e.g. Ryan *et al.* 2007; Evans *et al.* 2010, and references therein). Nor does this explain why such fossil ornithodirans as sympatric lambeosaurine hadrosaurs required large crests for species recognition, when sympatric members of closely related iguanodontian lineage did not.

Herd coherency does not require such elaborate structures: as detailed above, there are other ways of identifying conspecifics, even at greater ranges (e.g. sound can travel dozens of kilometres 'around' or 'through' objects while crests require line of sight and relative proximity). Crests exhibiting often subtle morphological differences and that are often small relative to the size of the animal (e.g. that of *Ceratosaurus*), cannot be considered an effective way of allowing animals to track their companions. Again, this issue does not appear to especially benefit members of extant clades where numerous similar taxa overlap in range, or alternatively where a single species lives in isolation from other members of its clade.

Non-sexual intraspecific signals

Here, definitions are harder to separate as, apart from active competition for mates (through display or ritualistic combat), ornithodiran ornaments may also play a role in non-sexual signalling (such as signalling danger etc.) (e.g. Farlow & Dodson 1975; Hopson 1975). In individuals with high social status, dominance can guarantee better territory, better access to resources and/or access to higher quality resources. These factors may allow the individual to enhance its fitness, and thus be more successful at producing more and higher quality offspring. While, therefore, the apparent use of the crest might not be directly sexually driven, the acquisition of resources could be considered an indirect form of sexual competition.

In hadrosaurs, the hollow, chambered crest may have performed an acoustic function (Weishampel 1981a,b). Although this has been questioned – Sullivan & Williamson (1999) were sceptical of an acoustic role for the tube-like crest of *Parasaurolophus* – we note that one of the most common roles of broadcast (long distance) vocalizations in vertebrates is sexual signalling (e.g. Bradbury & Vehrencamp 1998).

Other biomechanical functions

Clearly some cranial crests might provide mechanical advantage in strengthening the skull (e.g. *Anhanguera*,

Fastnacht 2007). For pterosaur crests especially, a number of biomechanically advantageous hypotheses have been suggested. Suggestions such as adding stability to flight (see Frey *et al.* 2003) or acting as a balance for the skull while skim-feeding (Kellner & Campos 2002) can be ruled out through experimental analysis: both suggested functions have proved poor explanations of structure when subjected to experimental analysis (Humphries *et al.* 2007; Elgin *et al.* 2008).

Discussion

Despite the numerous studies reviewed here, much uncertainty continues to surround the evolution and function of non-avialan ornithodiran crests. Although both theoretical and analytical studies have examined the possible functional roles of crests and ornaments (e.g. Farlow & Dodson 1975; Hopson 1975; Carpenter 1997; Farke *et al.* 2009), few of these hypothesized functions have withstood critical analysis. However, sexual selection or social dominance has been largely overlooked, or has been ruled out for reasons that are inappropriate in the light of modern sexual selection theory. We contend that, contrary to the view presented (or implicit) in many studies, sexual selection (and, notably, mutual sexual selection) was potentially prevalent across Ornithodira and was perhaps the dominant force behind the evolution of their cranial crests. At the very least this overlooked hypothesis should be strongly considered as a viable explanation in future analyses and discussions.

Our review suggests that little evidence supports existing hypotheses for crest function in most taxa, beyond social signalling and sexual selection (both of which are of course potentially linked). Caution must be used when dealing with small sample sizes, especially for organisms that are not represented in the extant fauna and exhibit great diversity in bauplan and cranial morphology. With these caveats in mind, we suggest that several aspects of ornithodiran reproductive behaviour can be directly linked to cranial ornamentation.

Ornithodiran ornamental evolution

Cranial crests are notably present in both pterosaurs and non-avialan dinosaurs. Although the two clades are close relatives (Benton 2004), the precise affinities of Pterosauria remain enigmatic (e.g. Hone & Benton 2007, 2008), and Pterosauria and Dinosauria are separated by a number of crestless taxa. (Sereno (1991) noted that *Scleromochlus*, an ornithodiran often intimated in pterosaur origins, may possess a small

cranial crest: this was not, however, confirmed in Benton's (1999) review of this taxon). While the crests present in some clades are often similar in structure or composition, it is clear that the crests of the various respective lineages evolved independently.

Nevertheless, the presence of diverse cranial crests in both dinosaurs and pterosaurs suggest a certain cranial plasticity in both groups and could be considered circumstantial evidence for a recent shared ancestry. (Horner & Goodwin (2009) even suggested exceptional intraspecific plasticity in some ornithodiran lineages). However, while the genetic origins of these crests may lie in shared ancestry, their continued function and evolution as social signals should be considered examples of parallel evolution.

Ornithodiran mutual sexual selection?

Sexual selection has been posited in the origin and maintenance of ornithodiran crests but has frequently been overlooked in analyses of crest function. This is despite the fact that many crests cannot have functioned in combat or defence, would have been too small to serve as warning signals or thermoregulatory structures, and do not seem to have been under selection for a biomechanical role. Some form of signalling remains the most viable hypothesis for the function of a great many crests: while we recognize the difficulty inherent in testing such functions, what evidence exists (namely late appearance during ontogeny and profound ontogenetic change) provides strong support. The ontogeny of ornithodiran cranial crests is consistent with the intraspecific mate competition hypothesis, but was also used to support the species recognition hypothesis (Padian & Horner 2011a). The fact that skeletal sexual dimorphism appears absent in most crested ornithodirans has resulted in the erroneous conclusion that sexual signalling and sexual selection could not be responsible for crest evolution, and hence that species recognition is the most reasonable interpretation (Padian and Horner 2011a,b). This, however, ignores the phenomenon of mutual sexual selection.

It has been argued that several dinosaurs, including *Protoceratops andrewsi*, *Agujaceratops mariscalensis* and various lambeosaurine hadrosaurs exhibit sexual dimorphism in cranial ornamentation (Brown & Schlaikjer 1940; Hopson 1975; Dodson 1976; Lehman 1990, 2007). However, the allegedly dimorphic *Corythosaurus* are not contemporaneous and almost certainly represent distinct species (Gates *et al.* 2007; see also Evans *et al.* 2010 and references therein) while the supposed sexual dimorphism reported in ceratopsians is subtle and continuous. Certainly other ornithodirans are known from numerous specimens where all

adults are apparently crested and skeletal dimorphism is not evident (e.g. ornithocheiroid and tapejarid pterosaurs, *Ceratosaurus*, oviraptorids). It appears that adult individuals of both sexes were similarly ornamented: given the similarities in cranial ornamentation, we must conclude that the crests in both sexes performed the same function in the same manner.

Mutual sexual selection is clearly difficult to establish for any fossil taxon. Nevertheless, some observations indicate that mutual sexual selection is a likely candidate factor in the evolution of at least some crested ornithodirans. An analogy can be made with those extant taxa in which both males and females are ornamented, yet mutual sexual selection is not apparently in operation: for example, those bovids in which both sexes have horns (e.g. *Damaliscus*, *Connochaetes*, *Taurotragus*, *Tragelaphus eurycerus*, *Syncerus*, *Bison*). Although few ornamented female bovids overtly compete for males (e.g. see Bro-Jørgensen 2002), many have ornaments distinguishable from those of males (female horns are less complex than those of males) and many use their horns in different fashion from those of males (female horns are consistent with a stabbing, anti-predator function, not a role in ritualized grappling and fighting – Caro *et al.* 2003), as demonstrated by higher rates of horn breakage in males despite their greater robustness (Packer 1983). While the normal reaction of a female to a possible predator would be to flee, they are often unwilling or unable to do so when defending a calf (Berger 1978; Estes & Estes 1979).

Non-avialian dinosaurs appear to have been predominantly r-selected, with post-hatching parental care being short or absent; the defence of juveniles can thus be assumed rare or absent (although some evidence for this exists: e.g. Varricchio *et al.* 2007). Furthermore, defence would only have been possible by those taxa exhibiting structures that could be used in combat (e.g. hadrosaurs, known to have practised post-hatching parental care, could not have used their crests to defend offspring from predators). While horned females are present in ca. 50% of African antelopes (Packer 1983), sexual dimorphism is still evident in body size, with males being larger.

In short, therefore, the pattern of ornamentations and inferred behaviours of non-avialian ornithodirans at least allow the possibility of mutual sexual selection. Males and females are similarly crested, with their crests (including horns) being similar in size, shape and, by extension, inferred function. Part of the motivation for our review is that palaeontologists seem largely unaware that the status of mutual sexual selection has been changing rapidly within behavioural ecology. Theoretical models show it to be expected under certain (not unduly restrictive) circumstances, while

empirical studies on various (mainly avian) taxa have shown how the same traits function as signals of quality, used in mate choice, in both sexes. The view that females alone choose mates (or are passive responders to male hierarchies determined by dominance interactions) while males are indiscriminate 'copulation maximizers' has been superseded. There are many circumstances under which male mating time and effort are limited, and/or female quality (as it translates into reproductive output) vary substantially, and under these conditions discriminating male mate choice is expected. In a nutshell, if a trait signals a quality of value to a mate (be it direct, such as care of young or defence from harassment, or indirect such as heritable disease resistance) then under these conditions it would be surprising not to see the same signalling trait present in both sexes and hence used in mate choice. Equivalently, if a trait is a reliable signal of resource holding potential, and if both sexes experience intrasexual conflict over resources (food, nesting sites, mates), then it would be surprising not to see the same signalling trait used in intrasexual conflict by both sexes. While sexual dimorphism is a convenient (but imperfect) clue that sexual selection is at work, it is not a defining hallmark.

Theropod behaviour and feather origins

A large number of fossil theropod taxa are crested, and the crests they exhibit are variable in morphology and position. Although such social behaviour as group hunting has been inferred for some non-avialan theropods (Ostrom 1972, 1990; Currie 1998), they have mostly been regarded as primarily solitary (see Molnar & Farlow 1990). However, the extensive ornamentation seen within non-avialan theropods suggests that members of at least some lineages engaged in frequent social interaction. As noted above, large visual signals present on a predatory species can potentially warn prey of the predator's approach and thus might be a selective disadvantage unless there were strong social benefits associated with such signals: this would be unlikely in a truly solitary species.

The presence of cranial ornamentation among diverse theropods suggests some level of social behaviour. This may not necessarily have been 'sociality' (i.e. group living) but, at least, frequent social interactions, and opens up the possibility of living in groups, meeting for social events (e.g. lekking, as suggested by Molnar & Farlow 1990), or being regularly involved in disputes over territory or resources (e.g. see evidence of intraspecific combat in Tanke & Currie 2000). Individuals of either sex would obviously do well to display their fitness or dominance via a signal rather than combat. While the case for theropod sociality as

imagined by some authors (Ostrom 1972, 1990; Currie 1998) has almost certainly been overstated (see Roach & Brinkman 2007), the presence of occasional social hunting in the Komodo dragon *Varanus komodoensis*, some crocodilians, and such birds as pelicans, caracaras and ground hornbills (Fitz Simmons 1962; Auffenberg 1981; Whiteacre *et al.* 1982; Yamashita 1991) at least raises the possibility that Mesozoic theropods of some species engaged in such behaviours as social hunting on occasion.

Of great importance to the possibility of sexual signalling is the origin and evolution of feathers. Much interest has surrounded the possible function of feathers before they were used for flight (e.g. Mayr 1960; Hopp & Orsen 2004). Given our inferences about the importance of signalling in dinosaurs with cranial ornaments, it is notable that cranial ornaments are almost entirely absent in those theropod clades known to possess feathers (Fig. 6). At the time that integumentary structures that can be used as specialized display organs appear and diversify, cranial crests all but vanish. Did feathers replace crests in coelurosaurian theropods?

There are several obvious benefits that feathers have relative to fixed bony crests. Feathers can be lost and re-grown as necessary (especially allowing seasonal changes), they can be highly coloured and present a wide variety of patterns, their complex anatomy might facilitate the expression of complex patterns relative to skin, they can be raised or lowered (and thus be made conspicuous or cryptic as occasion demands), and they are multifunctional, playing thermoregulatory and locomotory roles in addition to display.

We suggest that theropods would have benefited by transferring display functions from bony cranial ornaments to feathers and hypothesize that this may have facilitated the radical transition from crests to feathers. Several Cretaceous theropod taxa preserve integumentary structures that can be interpreted as functioning
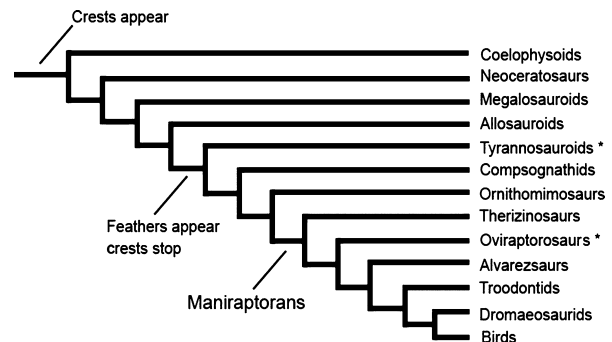

Fig. 6. Presence of bony cranial crests and feathers/protofeathers in theropods. Note the general lack of overlap between the two putative display structures with only tyrannosauroids and oviraptorosaurs having both (marked with an asterisk). Tree based on Lloyd *et al.* (2008).

in display, including the long remiges and tail fan of the oviraptorosaur *Caudipteryx* (Zhou & Wang 2000; Zhou *et al.* 2000) and the strap-like tail structures of the scansoriopterygid *Epidexipteryx* (Zhang *et al.* 2008). Preserved pigment traces indicate that bold patterns were present on the feathers or integumentary fibres of at least some fossil maniraptorans (Li *et al.* 2010; Zhang *et al.* 2010). Furthermore, Sullivan *et al.* (2010) proposed that the flexible wrists typical of birds appeared early in maniraptoran evolution to protect their remiges from damage; a proposal which could support the idea that these structures had a role in signal or display.

This transition is not absolute. Tyrannosauroids include taxa that possess both protofeathers and bony crests (Xu *et al.* 2004) as well as crested taxa without feathers (Larson 2008). While some forms (including *Proceratosaurus* and *Guanlong*) had relatively large crests (Xu *et al.* 2006), the crests of most taxa are limited to small ridges and bosses. In addition, a number of oviraptorosaur species possess bony cranial ornaments (Osmólska *et al.* 2004): the presence of feathers in basal oviraptorosaurs and other maniraptorans indicates that such taxa were fully feathered. This anomaly is currently unexplained, but we do not feel it detracts from the overall observation that feathers often occur where cranial ornaments do not and *vice versa* (just as cassowaries, guans, hornbills and curassows are unusual among birds in bearing bony crests).

Finally, the recent discovery of an ornithischian dinosaur with integumentary structures that are similar in some regards to protofeathers (Zheng *et al.* 2009) raises additional complexity. These structures may or may not be homologous with the protofeathers of theropods, or pycnofibres of pterosaurs (Kellner *et al.* 2009; Zheng *et al.* 2009). If these structures are indeed homologous, this implies that basal theropods and other saurischians and other dinosaurs may also have possessed integumentary fibres of some form. However, given that basal coelurosaurs (e.g. *Sinosauropteryx* and *Juravenator*) have short, simple protofeathers, it is likely that more basal theropods lacked any kind of integumentary structures that could be used for signalling any more than their scales could. The short and simple pterosaurian body fibres were clearly not mutually exclusive with large cranial crests.

We hypothesize, therefore, that in addition to other putative functions, feathers in non-avialian dinosaurs may have had an important role in signalling. Given their apparent superiority over fixed cranial crests, they may have rapidly superseded crests as the primary form of signalling. While oviraptorosaurs and several neornithine lineages represent exceptions, this hypothesis is supported by what appears to be a rapid switch from bony crests to feathers observed in the theropod tree.

Lack of crests in sauropods

The apparent absence of cranial ornamentation in sauropodomorphs is interesting in view of the presence, and indeed prevalence, of crests in other dinosaur lineages. It is a curious coincidence that almost all members of this clade are long necked and mostly very large (maximum lengths for some species may exceed 40 m). It is tempting to speculate that sauropodomorphs never evolved cranial ornamentation, favouring instead a reliance on neck length and/or gigantism for intraspecific sexual or social display (Senter 2007; Taylor *et al.* 2011). Perhaps supporting this suggestion is the fact that one of the few suspected cases of sexual ornamentation in sauropodomorphs – the presence of immense paired vertebral spines in the Argentinean diplodocoid *Amargasaurus cazaui* – is limited to the neck, and occurs in a clade (Dicraeosauridae) characterized by an unusually short neck (Salgado & Bonaparte 1991) and elongate neural spines.

Senter (2007) proposed that sauropod necks were indeed used as sexual signals and did not function primarily in increasing foraging range. This was based on analogy with the (far from widely accepted) hypothesis that the elongate necks of giraffes may function primarily as secondary sexual characteristics (Simmons & Scheepers 1996). However, evaluation shows that this proposal is poorly founded and that a role in foraging better explains the evolution of neck length in these dinosaurs (Taylor *et al.* 2011). It is also worth reiterating that some sauropods (notably brachiosaurids) do possess cranial structures that can be interpreted as ornaments and, furthermore, that the record of sauropod skulls is poor. While it is possible that cranial ornaments were largely replaced among sauropodomorphs with an alternate signal, possible crests (either cranial or cervical) are known in the group, and their presence elsewhere in the clade cannot be ruled out.

Loss of ceratopsian ornaments

The early evolution, and prevalence, of cranial ornamentation in marginocephalians suggests that the elaboration of cranial display organs was a common theme in the evolution of the clade. However, the hypothesis that ceratopsian brow horns acted as sexual signals becomes more interesting in view of the fact that both of the major clades that exhibit this character (Chasmosaurinae and Centrosaurinae) lost it during their evolution (e.g. see Ryan 2007). It is tempting to compare this with Wiens's (1999, 2001) conclusion, inspired by the repeated loss of conspicuous secondary sexual characters in male phrynosomatid lizards, that the losses of such characters may be common in some

clades. Elsewhere within vertebrates, repeated losses of male secondary sexual characters have been observed in fish, agamids (Ord & Stuart-Fox 2006), passerines and dabbling ducks (Omland 1997).

Conclusions

Despite extensive discussion of how cranial ornamentation might relate to sexual dimorphism and selection in both dinosaurs (e.g. Padian and Horner 2011a,b; Knell & Sampson 2011) and pterosaurs (e.g. Tomkins *et al.* 2010; Lü *et al.* 2011), little consensus has been reached. While the diversity of relevant taxa indicates that a variety of functions were doubtless involved, and while multifunctionailty cannot be excluded, we conclude that sexual signalling was likely an important – perhaps *the* most important or sole – driving force behind the evolution of many of these structures. Moreover, the overlooked issue of mutual sexual selection invalidates arguments claiming that the absence of dimorphism rules out a sexual selection function for cranial crests: the multitude of crested ornithodiran taxa may be mutually ornamented males and females. Testing such a proposal is difficult, with problems ranging from the limitations of the fossil record (both as goes sample sizes and recovering evidence for behaviour), disagreements over definitions, questions of appropriate methods and issues of multifunctionality. However, none of this is relevant if well known and potentially significant hypotheses remain unconsidered. It is also notable that despite the difficulty inherent in testing for mutual sexual selection in the fossil record, the issues listed above similarly afflict other hypotheses purported to explain behaviour and functionality linked to ornithodiran ornamentation.

Clearly, the anatomy and distribution of cranial crests in non-avialian ornithodirans have been the subject of rampant hypothesizing: while the free generation of hypotheses is a necessary prelude to focused data collection and testing, this should also be bounded by the available evidence, and by our understanding of evolutionary theory. Numerous ideas have been advanced that are not parsimonious in view of available evidence, and some concepts – such as sexual selection and especially mutual sexual selection – have been excluded *a priori* on false grounds.

The idea that Mesozoic ornithodirans experienced strong sexual selection and evolved numerous ornaments during their history should not perhaps come as a surprise. Extant theropod dinosaurs (birds) are famous for their sexual signals, be it in song, visual display or even constructions such as bowers. Birds also engage in behaviours known or suspected in many Mesozoic ornithodiran lineages, and possibly indicative of (mutual) sexual selection, such as gregarious behaviour, the expending of significant efforts in reproduction (large egg clutches, elaborate nest construction, and post-hatching parental care). In contrast, alternative reproductive strategies such as polygamy are tied to characteristics (such as larger bodied or more highly ornamented males) is generally not seen in Mesozoic ornithodirans.

This link to birds also provides secondary evidence for the origin (or at least elaboration) of feathers in dinosaurs, and thus ultimately the origin of flight and of birds themselves. The advent of the feather as an evolutionary novelty may have coincided with the loss of bony ornaments in theropods. Ornithodirans seemingly relied heavily on an acute sense of vision, and display structures such as crests or feathers can thus be expected to have played a large role in their courtship behaviour. This in turn may have prompted an increase in structural complexity and size: the evolution of the flight-capable feather and of flight itself may well have its roots in the evolution of ornithodiran sociosexual display.

References

Amundsen, T. 2000: Why are female birds ornamented? *Trends in Ecology & Evolution 15*, 149–155.

Andersson, M. 1994: *Sexual Selection*, 624 pp. Princeton University Press, Princeton.

Auffenberg, W. 1981: *The Behavioral Ecology of the Komodo Dragon*, 406 pp. University of Florida Press, Gainsville.

Bakker, R.T., Sullivan, R.M., Porter, V., Larson, P. & Sailsbury, S.J. 2006: *Dracorex hogwartsia*, n. gen, n. sp., a spiked, flat-headed pachycephalosaurid dinosaur from the Upper Cretaceous Hell Creek Formation of South Dakota. *In* Lucas, S.G. & Sullivan, R.M. (eds): *Late Cretaceous Vertebrates from the Western Interior*, 331–345. New Mexico Museum of Natural History and Science Bulletin 35.

Bennett, S.C. 1992: Sexual dimorphism of *Pteranodon* and other pterosaurs, with comments on cranial crests. *Journal of Vertebrate Paleontology 12*, 422–434.

Bennett, S.C. 1994: Taxonomy and systematics of the Late Cretaceous pterosaur *Pteranodon* (Pterosauria, Pterodactyloidea). *Occasional papers of the Natural History Museum, The University of Kansas, Lawrence* 169, 1–70.

Bennett, S.C. 1995: A statistical study of *Rhamphorhynchus* from the Solnhofen limestone of Germany: year-classes of a single large species. *Journal of Paleontology 69*, 569–580.

Benton, M.J. 1999: *Scleromochlus taylori* and the origin of dinosaurs and pterosaurs. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences 354*, 1423–1446.

Benton, M.J. 2004: Origin and relationships of Dinosauria. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 7–19. University of California Press, Berkeley.

Berger, J. 1978: Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. *Behavioral Ecology and Sociobiology 4*, 91–99.

Berglund, A., Bisazza, A. & Pilastro, A. 1996: Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society 58*, 385–399.

Birdsley, J.S. 2002: Phylogeny of the tyrant flycatchers (Tyrannidae) based on morphology and behaviour. *The Auk 11*, 715–734.

Bonduriansky, R. 2007: Sexual selection and allometry: a critical reappraisal of the evidence and ideas. *Evolution 61*, 838–849.

Bradbury, J.W. & Vehrencamp, S.L. 1998: *Principles of Animal Communication*, 882 pp. Sinauer, Sunderland.

Bramwell, C.D. & Fellgett, P.B. 1973: Thermal regulation in sail lizards. *Nature 242*, 203–205.

Bro-Jørgensen, J. 2002: Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences 99*, 9290–9293.

Brown, B. & Schlaikjer, E.M. 1940: The structure and relationships of *Protoceratops*. *Annals of the New York Academy of Sciences 40*, 133–266.

Caro, T.M., Graham, C.M., Stoner, C.J. & Flores, M.M. 2003: Correlates of horn and antler shape in bovids and cervids. *Behavioural Ecology and Socio-Biology 55*, 32–41.

Carpenter, K. 1997: Agonistic behavior in pachycephalosaurs (Ornithischia: Dinosauria): a new look at head-butting behavior. *Contributions to Geology, University of Wyoming 32*, 19–25.

Chapman, R.E., Weishampel, D.B., Hunt, G. & Rasskin-Gutman, D. 1997: Sexual Dimorphism in Dinosaurs. *In* Wolberg, D.L., Stump, E. & Rosenberg, G.D. (eds): *Dinofest International: Proceedings of a symposium held at Arizona State University*, 83–93, Philadelphia, Academy of Natural Sciences.

Colbert, E.H. 1948: Evolution of the horned dinosaur. *Evolution 2*, 145–163.

Colbert, E.H. 1955: *Evolution of the Vertebrates*, 501 pp. Wiley, New York.

Cronin, H. 1991: *The Ant and the Peacock*, 490 pp. Cambridge University Press, Cambridge.

Currie, P.J. 1998: Possible evidence of gregarious behaviour in tyrannosaurids. *Gaia 15*, 217–227.

Czerkas, S.A. & Ji, Q. 2002: A new rhamphorhynchoid with a head crest and complex integumentary structures. *The Dinosaur Museum Journal 1*, 15–41.

Darwin, C. 1871: *The Descent of Man, and Selection in Relation to Sex*, 501 pp. John Murray, London.

Dodson, P. 1975: Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Systematic Zoology 24*, 37–54.

Dodson, P. 1976: Quantitative aspects of relative growth and sexual dimorphism in *Protoceratops*. *Journal of Paleontology 50*, 929–940.

Dodson, P. 1990: On the status of the ceratopsids *Monoclonius* and *Centrosaurus*. *In* Carpenter, K. & Currie, P.J. (eds): *Dinosaur Systematics: Approaches and Perspectives*, 231–243. Cambridge University Press, Cambridge.

Dodson, P. & Currie, P.J. 1990: Neoceratopsia. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 593–618. University of California Press, Berkeley.

Dodson, P., Forster, C.A. & Sampson, S.D. 2004: Ceratopsidae. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 494–516. University of California Press, Berkeley.

Elgin, R.A., Grau, C., Palmer, C., Hone, D.W.E., Greenwell, D. & Benton, M.J. 2008: Aerodynamic characters of the cranial crest in *Pteranodon*. *Zitteliana B 28*, 169–176.

Erickson, G.M., van Kirk, S.D., Su, J., Levenston, M.E., Caler, W.E. & Carter, D.R. 1996: Bite–force estimation for *Tyrannosaurus rex* from bone–marks. *Nature 382*, 706–708.

Estes, R.D. & Estes, R.K. 1979: The birth and survival of wildebeest calves. *Zeitschrift für Tierpsychologie 50*, 45–95.

Evans, D.C., Bavington, R. & Campione, N.E. 2010: An unusual hadrosaurid braincase from the Dinosaur Park Formation and the biostratigraphy of *Parasaurolophus* (Ornithischia: Lambeosaurinae) from Southern Alberta. *Canadian Journal of Earth Sciences 46*, 791–800.

Farke, A.A. 2004: Horn use in *Triceratops* (Dinosauria: Ceratopsidae): testing behavioral hypotheses using scale models. *Palaeontologia Electronica 7*, 1–4.

Farke, A.A. 2011: Anatomy and taxonomic status of the chasmosaurine ceratopsid *Nedoceratops hatcheri* from the Upper Cretaceous Lance Formation of Wyoming, USA. *PLoS ONE 6*, e16196.

Farke, A.A., Wolff, E.D.S. & Tanke, D.H. 2009: Evidence of combat in *Triceratops*. *PLoS ONE 4*, e4252.

Farke, A.A., Chapman, R.E. & Anderson, A. 2010: Modelling structural properties of the frill of *Triceratops*. *In* Ryan, M.J., Chinnery-Allgeier, B.J. & Eberth, D. (eds): *New Perspectives on Horned Dinosaurs*, 264–270. Indiana University Press, Bloomington.

Farlow, J.O. & Dodson, P. 1975: The behavioural significance of frill and horn morphology in certopsian dinosaurs. *Evolution 29*, 53–361.

Fastnacht, M. 2007: *Why Did They Do It That Way? A Study of the Pterosaur Skull Construction and Their Evolutionary Pathways*. Abstracts of the Flugsaurier Wellnhofer Pterosaur Meeting, Munich.

Fitz Simmons, V. 1962: *Snakes of Southern Africa*, 423 pp. MacDonald, London.

Folch, A. 1992: Family Casuariidae (Cassowaries). *In* Del Hoyo, J., Elliott, A. & Sargatal, J. (eds): *Handbook of the Birds of the World. Volume 1: Ostriches to Ducks*, 90–97. Lynx Edicions, Barcelona.

Forster, C.A. 1997: Hadrosauridae. *In* Currie, P.J. & Padian, K. (eds): *Encyclopedia of Dinosaurs*, 293–299. Academic Press, San Diego.

Frey, E., Tischlinger, H., Buchy, M.-C. & Martill, D.M. 2003: New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion. *In* Buffetaut, E. & Mazin, J.-M. (eds): *Evolution and Palaeobiology of Pterosaurs*, 233–282. Geological Society of London, Special Publications 217, London.

Galton, P.M. 1970: Pachycephalosaurids – dinosaurian battering rams. *Discovery 6*, 23–32.

Galton, P.M. 1971: A primitive dome-headed dinosaur (Ornithischia: Pachycephalosauridae) from the lower Cretaceous of England, and the function of the dome in pachycehalosaurids. *Journal of Paleontology 45*, 40–47.

Gaston, A.J. & Jones, I.L. 1998: *The Auks*, 349 pp. Oxford University Press, Oxford.

Gates, T.A., Sampson, S.D., Delgado de Jesús, C.R., Zanno, L.E., Eberth, D., Hernandez-Rivera, R., Aguillón Martínez, M.C. & Kirkland, J.I. 2007: *Velafrons coahuilensis*, a new lambeosaurine hadrosaurid (Dinosauria: Ornithopoda) from the Late Campanian Cerro del Pueblo Formation, Coahuila, Mexico. *Journal of Vertebrate Paleontology 27*, 917–930.

Goodwin, M.B. & Horner, J.R. 2004: Cranial histology of pachycephalosaurs (Ornithischia: Marginocephalia) reveals transitory structures inconsistent with head-butting behavior. *Paleobiology 30*, 253–267.

Goodwin, M.B., Buchholtz, E.M. & Johnson, R.E. 1998: Cranial anatomy and diagnoses of *Stygimoloch spinifer* (Ornithischia: Pachycephalosauria) with comments on cranial display structures in agonistic behavior. *Journal of Vertebrate Paleontology 18*, 363–375.

Goodwin, M.B., Clemens, W.A., Horner, J.R. & Padian, K. 2006: The smallest known *Triceratops* skull: new observations on ceratopsid cranial anatomy and ontogeny. *Journal of Vertebrate Paleontology 26*, 103–112.

Happ, J. 2008: An analysis of predator-prey behavior in a head-to-head encounter between Tyrannosaurus rex and *Triceratops*. *In* Larson, P. & Carpenter, K. (eds): Tyrannosaurus rex *the Tyrant King*, 352–370. Indiana University, Bloomington.

Hoefs, M. 2000: The thermoregulatory potential of *Ovis* horn cores. *Canadian Journal of Zoology 78*, 1419–1426.

Holtz, T.R. Jr, Molnar, R.E. & Currie, P.J. 2004: Basal Tetanurae. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 71–110. University of California Press, Berkeley.

Hone, D.W.E. & Benton, M.J. 2007: An evaluation of the phylogenetic relationships of the pterosaurs among archosauromorph reptiles. *Journal of Systematic Palaeontology 5*, 465–469.

Hone, D.W.E. & Benton, M.J. 2008: Contrasting supertrees and total-evidence methods: pterosaur origins. *Zitteliana B 28*, 35–60.

Hone, D.W.E. & Rauhut, O.W.M. 2010: Feeding behaviour and bone utilization by theropod dinosaurs. *Lethaia 43*, 232–244.

Hopp, T.P. & Orsen, M.J. 2004: Dinosaur brooding behaviour and the origin of feathers. *In* Currie, P.J., Koppelhus, E.B., Shugar, M.A. & Wright, J.L. (eds): *Feathered Dragons: Studies on the Transition From Dinosaurs to Birds*, 234–250. Indiana University Press, Bloomington.

Hopson, J.A. 1975: The evolution of cranial display structures in hadrosaurian dinosaurs. *Paleobiology 1*, 21–43.

Horner, J.R. & Goodwin, M.B. 2006: Major cranial changes in *Triceratops*. *Proceedings of the Royal Society, B 273*, 2757–2761.

Horner, J.R. & Goodwin, M.B. 2009: Extreme cranial ontogeny in the Upper Cretaceous dinosaur *Pachycephalosaurus*. *PLoS ONE 4*, e7626.

Horner, J.R., Weishampel, D.B. & Forster, C.A. 2004: Hadrosauridae. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 438–463. University of California Press, Berkeley.

Humphries, S., Bonser, R.H.C., Witton, M.P. & Martill, D.M. 2007: Did pterosaurs feed by skimming? Physical modelling and anatomical evaluation of an unusual feeding method. *PLoS Biology 5*, 1–9.

Hunt, S., Cuthill, I.C., Bennett, A.T.D. & Griffiths, R.M. 1999: Preference for ultraviolet partners in the blue tit. *Animal Behaviour 58*, 809–815.

Huxley, J.S. 1914: The courtship habits of the great crested grebe *Podiceps cristatus*; with an addition to the theory of sexual selection. *Proceedings of the Zoological Society of London 35*, 491–562.

Isles, T.E. 2010: The socio-sexual behaviour of extant archosaurs: implications for understanding dinosaurs. *Historical Biology 21*, 139–214.

Jacobs, G.H. & Rowe, M.P. 2004: Evolution of vertebrate colour vision. *Clinical and Experimental Optometry 87*, 206–216.

Johnstone, R.A. 1997: The tactics of mutual mate choice and competitive search. *Behavioural Ecology and Sociobiology 40*, 51–59.

Johnstone, R.A., Reynolds, J.D. & Deutsch, J. 1996: Mutual mate choice and sex differences in choosiness. *Evolution 50*, 1382–1391.

Jones, I.L. & Hunter, F.M. 1993: Mutual sexual selection in a monogamous seabird. *Nature 362*, 238–239.

Jones, I.L. & Hunter, F.M. 1999: Experimental evidence for mutual inter- and intra-sexual selection favouring a crested auklet ornament. *Animal Behaviour 57*, 521–528.

Kellner, A.W.A. & Campos, D.A. 2002: The function of the cranial crest and jaw of a unique pterosaur from the Early Cretaceous of Brazil. *Science 297*, 389–392.

Kellner, A.W.A., Wang, X., Tischlinger, H., Campos, D.A., Hone, D.W.E. & Meng, X. 2009: The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathidae) and the structure of the pterosaur wing membrane. *Proceedings of the Royal Society, Series B 277*, 321–329.

Knell, R.J. & Sampson, S. 2011: Bizarre structures in dinosaurs: species recognition or sexual selection? A response to Padian and Horner. *Journal of Zoology 283*, 18–22.

Kobayashi, Y. & Barsbold, R. 2005: Reexamination of a primitive ornithomimosaur *Garudimimus brevipes* Barsbold, 1981 (Dinosauria: Theropoda), from the Late Cretaceous of Mongolia. *Canadian Journal of Earth Sciences 42*, 1501–1521.

Kokko, H. & Johnstone, R.A. 2002: Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society, London B 357*, 319–330.

Komdeur, J., Oorebeek, M., van Overveld, T. & Cuthill, I.C. 2005: Mutual ornamentation, age, and reproductive performance in the European starling. *Behavioral Ecology 16*, 805–817.

Kraaijeveld, K., Gregurke, J., Hall, C., Komdeur, J. & Mulder, R.A. 2004: Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behavioral Ecology 15*, 380–389.

Kraaijeveld, K., Kraaijeveld-Smit, F.J.L. & Komdeur, J. 2007: The evolution of mutual ornamentation. *Animal Behaviour 74*, 657–677.

Larson, N.L. 2008: One hundred years of *Tyrannosaurus rex*: the skeletons. *In* Larson, P. & Carpenter, K. (eds): Tyrannosaurus rex, *The Tyrant King*, 1–55. Indiana University Press, Bloomington.

Lehman, T.M. 1990: The ceratopsian subfamily Chasmosaurinae: sexual dimorphism and systematics. *In* Carpenter, K. & Currie, P.J. (eds): *Dinosaur Systematics: Approaches and Perspectives*, 221–229. Cambridge University Press, Cambridge.

Lehman, T.M. 2007: Growth and population age structure in the horned dinosaur. *In* Carpenter, K. (ed.): *Chasmosaurus. Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs*, 259–317. Indiana University Press, Carpenter.

Li, Q., Gao, K.-Q., Vinther, J., Shawkey, M.D., Clarke, J.A., D'Alba, L., Meng, Q., Briggs, D.E.G. & Prum, R.O. 2010: Plumage colour patterns of an extinct dinosaur. *Science 326*, 1369–1372.

Littlejohn, M.J. 1999: The evolution and breakdown of homogamy. *In* Foster, S.A. & Endler, J.A. (eds): *Geographic Variation in Behavior*, 209–233. Oxford University Press, Oxford.

Lloyd, G.T., Davis, K.E., Pisani, D., Tarver, J.E., Ruta, M., Sakamoto, M., Hone, D.W.E., Jennings, R. & Benton, M.J. 2008: Dinosaurs and the Cretaceous terrestrial revolution. *Proceedings of the Royal Society of London B 275*, 2483–2490.

Lockley, M., Harris, J.D. & Mitchell, L. 2008: A global overview of pterosaur ichnology: tracksite distribution in time and space. *Zitteliana B 28*, 185–198.

Lü, J., Unwin, D.M., Deeming, D.C., Jin, X., Liu, Y. & Ji, Q. 2011: An egg-adult association, gender, and reproduction in pterosaurs. *Science 331*, 321–324.

Mack, A.L. & Jones, J. 2003: Low-frequency vocalizations by cassowaries *Casuarius* spp. *The Auk 120*, 1062–1068.

Main, R.P., Padian, K. & Horner, J.R. 2000: Comparative histology, growth and evolution of archosaurian osteoderms: Why did *Stegosaurus* have large dorsal plates? *Journal of Vertebrate Paleontology 20*(suppl 56A), 20.

Makovicky, P.J. & Norell, M.A. 2006: *Yamaceratops dorngobiensis*, a new primitive ceratopsian (Dinosauria: Ornithischia) from the Cretaceous of Mongolia. *American Museum Novitates 3530*, 1–42.

Martill, D.M. & Naish, D. 2006: Cranial crest development in the azhdarchoid pterosaur *Tupuxuara*, with a review of the genus and tapejarid monophyly. *Palaeontology 49*, 925–941.

Mayr, E. 1960: The emergence of evolutionary novelties. *In* Tax, S. (ed.): *The Evolution of Life*, 349–380. University of Chicago Press, Chicago.

Mayr, E. 1970: *Populations, Species and Evolution*, 348 pp. Harvard University Press, Cambridge.

Measey, G.J., Hopkins, K. & Tolley, K.A. 2009: Morphology, ornaments and performance in two chameleon ecomorphs: is the casque bigger than the bite? *Zoology 112*, 217–226.

Molnar, R.E. & Farlow, J.O. 1990: Carnosaur paleobiology. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 210–224. University of California Press, Berkeley.

Norman, D.B. 1991: *The Illustrated Encyclopaedia of Dinosaurs*, 208 pp. Salamander Books, London.

Norman, D.B., Witmer, L.M. & Weishampel, D.B. 2004: Basal Ornithischia. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 325–333. University of California Press, Berkeley.

Omland, K.E. 1997: Examining two standard assumptions of ancestral reconstruction: repeated loss of dichromatism in dabbling ducks Anatini. *Evolution 5*, 1636–1646.

Ord, T.J. & Stuart-Fox, D. 2006: Ornament evolution in dragon lizards: multiple gains and widespread losses reveal a complex history of evolutionary change. *Journal of Evolutionary Biology 19*, 797–808.

Osmólska, H., Currie, P.J. & Barsbold, R. 2004: Oviraptorosauria. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 165–183. University of California Press, Berkeley.

Ostrom, J.H. 1972: Were some dinosaurs gregarious? *Palaeogeography, Palaeoclimatology, Palaeoecology 11*, 287–301.

Ostrom, J.H. 1990: Dromaeosauridae. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 269–279. University of California Press, Berkeley.

Packer, C. 1983: Sexual dimorphism: the horns of African antelopes. *Science 221*, 1191–1193.

Padian, K. & Horner, J. 2011a: The evolution of 'bizarre structures' in dinosaurs: biomechanics, sexual selection, social selection, or species recognition? *Journal of Zoology 283*, 3–17.

Padian, K. & Horner, J. 2011b: The definition of sexual selection and its implications for dinosaurian biology. *Journal of Zoology 283*, 23–27.

Paul, G.S. 1988: *Predatory Dinosaurs of the World*, 464 pp. Simon & Schuster, New York.

Pérez-Moreno, B.P., Sanz, J.L., Buscalioni, A.D., Moratall, J.J., Ortega, F. & Rasskin-Gutman, D. 1994: A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature 370*, 363–367.

Prudic, K.L., Jeon, C., Cao, H. & Monteiro, A. 2011: Developmental plasticity in sexual roles of butterfly species drives mutual sexual ornamentation. *Science 331*, 73–75.

Ptacek, M.B. 2000: The role of mating preferences in shaping interspecific divergence in mating signals in vertebrates. *Behavioural Processes 51*, 111–134.

Roach, B.T. & Brinkman, D.L. 2007: A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. *Bulletin of the Peabody Museum of Natural History 48*, 103–138.

Romer, A.S. 1956: *Osteology of the Reptiles*, 2nd edn, 772 pp. University of Chicago Press, Chicago.

Ruxton, G.D., Sherratt, T.N. & Speed, M.P. 2004: *Avoiding Attack*, 251 pp. Oxford University Press, Oxford.

Ryan, M.J. 2007: A new basal centrosaurine ceratopsid from the Oldman Formation, southeastern Alberta. *Journal of Paleontology 91*, 376–396.

Ryan, M.J., Holmes, R. & Russell, A.P. 2007: A revision of the Late Campanian centrosaurine ceratopsid *Styracosaurus* from the Western Interior of North America. *Journal of Vertebrate Paleontology 27*, 944–962.

Salgado, L. & Bonaparte, J.F. 1991: Un nuevo sauropodo Dicraeosauridae, *Amargasaurus cazaui* gen. et sp. nov., de la Formacion La Amarga, Neocomiano de la Provincia del Neuquen, Argentina. *Ameghiniana 28*, 333–346.

Sampson, S.D. 1995: Horns, herds, and hierarchies. *Natural History 104*, 36–40.

Sampson, S.D. 2001: Speculations on the socioecology of ceratopsid dinosaurs (Ornithischia: Neoceratopsia). *In* Tanke, D.H. & Carpenter, C. (eds): *Mesozoic Vertebrate Life*, 263–276. Indiana University Press, Bloomington.

Senter, P. 2007: Necks for sex: sexual selection as an explanation for sauropod dinosaur neck elongation. *Journal of Zoology 271*, 45–53.

Sereno, P.C. 1986: Phylogeny of the bird-hipped dinosaurs order Ornithischia. *National Geographic Research 2*, 234–256.

Sereno, P.C. 1991: Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology 11*(Suppl 4), 1–49, *Memoir 2*.

Simmons, R.E. & Scheepers, L. 1996: Winning by a neck: sexual selection in the evolution of giraffe. *The American Naturalist 148*, 771–786.

Smith, N.D., Makovicky, P.J., Hammer, W.R. & Currie, P.J. 2007: Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society 151*, 377–421.

Snively, E. & Cox, A. 2008: Structural mechanics of pachycephalosaur crania permitted head-butting behaviour. *Palaeontologica Electronica 11*(13A), 17.

Spassov, N.B. 1979: Sexual selection and the evolution of horn-like structures of ceratopsian dinosaurs. *Palaeontology, Stratrigraphy and Litholog 11*, 37–48.

Stein, R.S. 1975: Dynamic analysis of *Pteranodon ingens*: a reptilian adaptation to flight. *Journal of Paleontology 49*, 534–548.

Stevens, K.A. 2006: Binocular vision in theropod dinosaurs. *Journal of Vertebrate Paleontology 26*, 321–330.

Sullivan, R.M. 2003: Revision of the dinosaur *Stegoceras* Lambe (Ornithischia, Pachycephalosauridae). *Journal of Vertebrate Paleontology 23*, 181–207.

Sullivan, R.M. & Williamson, T.E. 1999: A new skull of *Parasaurolophus* Dinosauria: Hadrosauridae from the Kirtland Formation of New Mexico and a revision of the genus. *New Mexico Museum of Natural History & Science Bulletin 15*, 1–52.

Sullivan, C., Hone, D.W.E., Xu, X. & Zhang, F. 2010: The asymmetry of the carpal joint and the evolution of wing folding in maniraptoran theropod dinosaurs. *Proceedings of the Royal Society, Series B 277*, 2027–2033.

Tanke, D.H. & Currie, P.J. 2000: Head biting behaviour in theropod dinosaurs: paleopathological evidence. *Gaia 15*, 167–184.

Taylor, R.A. 1960: The vascularity and possible thermoregulatory function of the horns in goats. *Physiological Zoology 39*, 127–139.

Taylor, M.T., Hone, D.W.E., Wedel, M.J. & Naish, D. 2011: The long necks of sauropods did not evolve primarily through sexual selection. *Journal of Zoology 285*, 150–161.

Tomkins, J.L., Lebas, N.R., Witton, M.P., Martill, D.M. & Humphries, S. 2010: Positive allometry and the prehistory of sexual selection. *The American Naturalist 176*, 141–148.

Trivers, R.L. 1972: Parental investment and sexual selection. *In* Campbell, B. (ed.): *Sexual Selection and the Descent of Man 1871–1971*, 136–179. Heinemann, London.

Tykoski, R.S. & Rowe, T. 2004: Ceratosauria. *In* Weishampel, D.B., Dodson, P. & Osmólska, H. (eds): *The Dinosauria*, 47–69. University of California Press, Berkeley.

Unwin, D.M. 2003: On the phylogeny and evolutionary history of pterosaurs. *In* Buffetaut, E. & Mazin, J.-M. (eds): *Evolution and Palaeobiology of Pterosaurs*, 139–190. Geological Society of London, Special Publications 217, London.

Unwin, D.M. 2005: *Pterosaurs From Deep Time*, 347 pp. Pi Press, New York.

Varricchio, D.J., Martin, A.J. & Katsura, Y. 2007: First trace and body fossil evidence of a burrowing, denning dinosaur. *Proceedings of the Royal Society B 274*, 1361–1368.

Varricchio, D.J., Moore, J.R., Erickson, G.M., Norell, M.A., Jackson, F.D. & Borkowski, J.J. 2008: Avian paternal care had dinosaur origin. *Science 322*, 1826–1828.

Weishampel, D.B. 1981a: The nasal cavity of lambeosaurine hadrosaurids (Reptilia: Ornithischia): comparative anatomy and homologies. *Journal of Paleontology 55*, 1046–1057.

Weishampel, D.B. 1981b: Acoustic analyses of potential vocalization in lambeosaurine dinosaurs Reptilia: Ornithischia. *Palaeobiology 7*, 252–261.

Welles, S.P. 1984: *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaeontographica A 185*, 85–180.

Wellnhofer, P. 1991: *The Illustrated Encyclopedia of Pterosaurs*, 192 pp. Salamander Books, London.

Wheeler, R.E. 1978: Elaborate CNS cooling systems in large dinosaurs. *Nature 275*, 441–443.

\Whiteacre, D., Ukrain, D. & Falxa, G. 1982: Notes on the hunting behavior and diet of the Crested Caracara in Northeastern Chiapas and Tabasco, Mexico. *The Wilson Bulletin 94*, 565–566.

Wiens, J.J. 1999: Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. *Proceedings of the Royal Society, B 266*, 1529–1535.

Wiens, J.J. 2001: Widespread loss of sexually selected traits: how the peacock lost its spots. *Trends in Ecology and Evolution 16*, 517–523.

Xu, X., Norell, M.A., Kuang, X., Wang, X., Zhao, Q. & Jia, C. 2004: Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature 431*, 680–684.

Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jia, C. & Zhao, Q. 2006: A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature 439*, 715–718.

Yamashita, C. 1991: Social fishing behavior in Paraguayan caiman. *CSG Newsletter 10*, 13.

Yokoyama, S. 2002: Molecular evolution of colour vision in vertebrates. *Gene 300*, 69–78.

Zhang, F., Zhou, Z.-H., Xu, X., Xaiolin, W. & Sullivan, C. 2008: A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. *Nature 455*, 1105–1108.

Zhang, F., Kearns, S.L., Orr, P.J., Benton, M.J., Zhou, Z., Johnson, D., Xu, X. & Wang, X. 2010: Fossilized melanosomes and the colour of Cretaceous dinosaurs and birds. *Nature 463*, 1075–1078.

Zhao, X.-J. & Currie, P.J. 1993: A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences 30*, 2027–2036.

Zheng, X.T., You, H.L., Xu, X. & Dong, Z. 2009: An Early Cretaceous heterodontosaurid with filamentous integumentary structures. *Nature 458*, 333–336.

Zhou, Z.-H. & Wang, X.-L. 2000: A new species of *Caudipteryx* from the Yixian Formation of Liaoning, northeast China. *Vertebrata Palasiatica 38*, 111–127.

Zhou, Z.-H., Wang, X.-L., Zhang, F.-C. & Xu, X. 2000: Important features of *Caudipteryx* – evidence from two nearly complete new specimens. *Vertebrata PalAsiatica 38*, 241–254.