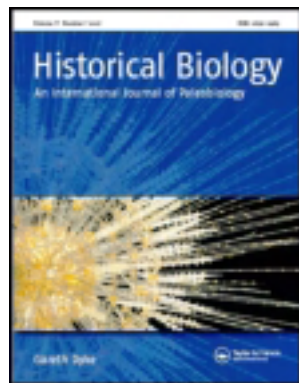


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The socio-sexual behaviour of extant archosaurs: implications for understanding dinosaur behaviour

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The socio-sexual behaviour of extant archosaurs: implications for understanding dinosaur behaviour

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Dinosaur behaviour has little legacy in the fossil record and the rarity of fossil soft tissues makes it difficult to evaluate. Indirect evidence from bonebeds, trackways, nesting traces and in-group comparisons with extant Archosauria suggests that the only substantive arguments to be made for dinosaur sociality concern cranial ornamentation and herding behaviour. There is currently no reliable method to determine gender from skeletal remains. Dinosaur reproductive anatomy was a unique combination of crocodilian and avian characters and extant models indicate that dinosaurs copulated using a reptilian 'leg over back' posture. Reliable evidence for post-hatching care in dinosaurs is lacking and extant archosaurs yield little insight. A hypothesis is proposed that for the majority of dinosaurs there was no post-hatching care provided which would have allowed adults energy acquisition that would otherwise have been required for defence and provisioning to be redirected towards growth and increased fecundity, both traits for which there is fossil evidence. Arguments suggesting that the more advanced aspects of extant avian care boasting an explicit coelurosaurian theropod origin are rejected as these behaviours appear unique to the Neornithes. Three ancestral care hypotheses are tested and none conform in a satisfactory manner with body fossil and ichnological evidence.

Keywords: dinosauria; mating; parental care; aves; crocodilians; reproduction

1. Introduction

Recently, it has become fashionable to portray a range of advanced avian post-hatching and nesting behaviours as having been explicitly present in theropod dinosaurs in both popular culture and science. Novels (e.g. Bakker 1996) and television documentaries (e.g. the Discovery Channel's 2003 four-part series *Dinosaur Planet*) represent many dinosaur taxa as maintaining lifelong pair bonds in multigenerational family units that live, learn and hunt in stable long-term groups. These views tend to be inspired by hypotheses, albeit presented in a less visually dramatic manner, commonly found in the scientific literature. Bakker (1997) argued that *Allosaurus* parents provisioned their offspring with carcasses dragged over long distances to 'dens' where the young could feed safely. Dromaeosaurids are often exclusively described as the dinosaurian equivalent of wolves with apparently sophisticated social structures deemed necessary for the effective pack hunting of larger prey (Bakker 1986; Maxwell and Ostrom 1995). A similar scenario was formally proposed for the tyrannosaurids *Albertosaurus* (Currie 1998) and *Daspletosaurus* (Currie et al. 2005a) in which both employed pack hunting and a sophisticated division of labour, with smaller and apparently faster juvenile members targeting faster moving prey. Similar ideas concerning long-term parental feeding and

nestbound altricial neonates have been suggested for hadrosaurids (e.g. Horner and Makela 1979; Horner 2000).

The phylogenetic relationships between extant avians and coelurosaurian theropods, in particular, have been well documented (e.g. Gauthier 1986; Holtz 1996; Dingus and Rowe 1998; Prum 2002), resulting in investigations of the origin of Neoaves parental-care systems. Extant archosaurs share ancestral characters such as calcareous eggs, nest construction and unique oviduct morphology (e.g. Mateus 1998; Carpenter 1999; Sato et al. 2005). Many investigators have applied these observations to extinct archosaurs, especially dinosaurs. It is argued that coelurosaurians, and *Troodon* and the oviraptorids in particular, employed direct contact incubation, used delayed incubation of their clutches and exhibited male-only care of nests. Furthermore, according to these views the most derived aspects of neognath parental behaviour and nest attendance were already present in and thus originated in theropods (e.g. see Larson 1998; Prum 2002; Varricchio and Jackson 2004b; Varricchio et al. 2008a; Zelenitsky and Therrien 2008). In this emerging consensus, theropods do not simply have an evolutionary relationship with avians, but are considered to be more or less interchangeable from both a social and behavioural perspective.

This modern tendency to propose behavioural patterns and social organisations that go far beyond what can

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be reasonably extrapolated from the fossil record, is in stark contrast to classic paleobiological investigations in which a more conservative approach was advanced (e.g. see Boucot 1990). But is there any evidence supporting the presence of sophisticated social behaviours observed in derived mammals such as Canidae and Primates? Does the fossil record support notions of dinosaurs enjoying advanced social organisation that included extended family structures? Is there any reason to consider that theropods were the behavioural and social equivalent of Neoaves? What reliable and unequivocal evidence is there for dinosaur socio-sexual (courtship, mating and parenting) behaviour? Investigating these types of activity in extinct organisms is hampered by a general lack of fossil preservation of either identifiable behaviour or soft tissues. Therefore, studies tend to focus on trackways, mass accumulations and other trace evidence (Molnar 1977; Weishampel 1995a). Further insights can be attained by means of in-group comparisons using extant phylogenetic bracketing, a method of inference in which an extinct taxon is compared to its nearest extant relatives based upon their position on a phylogenetic tree (see Witmer 1995).

This paper critically evaluates the current state of evidence by first reviewing the essential aspects of socio-sexual characteristics of extinct archosaurs and comparing them to those described for their extant relatives. Evaluations are then made as to whether ichnological evidence supports putative equivalent traits in dinosaurs and examines whether any relevance or insight can be gleaned from extant archosaurs. Videofilm records depicting the sexual behaviour and postures of several reptiles and mammals were evaluated to see if similar positioning would have been possible in dinosaurs. The evidence is brought together, and an inventory of both demonstrable and putative reproductive structures and behaviours is mapped onto a phylogeny of the Archosauria. An appraisal was undertaken to determine whether (1) dinosaurs, and coelurosaurians in particular, offer insights regarding the evolution of neognath post-hatching parental care and (2) if any understanding of extant avian parental care can be derived from the fossil record. Finally, the question as to whether the parental care in Crocodylia and Neoaves serves any relevance in terms of understanding what might have occurred in dinosaurs is discussed. As there appears to be little in the literature overtly critical of the current direction of the aforementioned trends, this paper approaches the issue from an ethological perspective.

2. Socio-sexual behaviour in dinosauria: evidence from paleontology

Although some aspects of dinosaur behaviour have been documented from fossil evidence (e.g. locomotion: Thulborn 1984; Farlow et al. 2000; Hutchinson and Garcia 2002;

Henderson 2006; Alexander 2008), it is obvious that the majority of dinosaur behaviour has no legacy in the fossil record. Furthermore, the rarity of soft tissue preservation makes it extremely difficult to evaluate putative socio-sexual behaviours in extinct dinosaurs. However, indirect evidence and clues can be gleaned from such varied sources as anatomy, bonebeds, trackways, paleopathology, nesting traces and in-group comparisons with extant Archosauria (e.g. Molnar 1977; Weishampel 1995a; Witmer 1995; Sampson 1997a). This evidence and any competing hypotheses of dinosaur behaviour are reviewed.

2.1 Evidence for gender determination in dinosaurs

The question of how to positively identify gender from often incomplete or damaged skeletons is a pressing concern in any discussion of reproductive behaviour in extinct vertebrates. The positive identity of gender is a key component in the understanding of possible social organisations, demographics and population dynamics and as such remains a 'holy grail' of dinosaur paleontology (e.g. Erickson et al. 2005). Distinguishing the gender of extinct taxa based wholly on fossil is by no means straightforward, as the entire process is plagued by confounding variables ranging from variations in preservation and taphonomy, [see Chapman et al. (1997) for a detailed discussion], although evidence may be found in skeletal dimorphism, which might reflect sexual dimorphism.

Sexual dimorphism is the circumstance in which males and females of a single species exhibit distinct physical differences such as size, gender-specific markings (patterns and/or colour) or the presence of ornamentation which may include horns, crests and display feathers (e.g. Alcock 1989; Grier and Burk 1992; Fairbairn 2007). This phenomenon is widespread throughout extant tetrapod groups and invertebrates and is usually expressed in terms of the male demonstrating a larger physical size, (e.g. northern elephant seal *Mirounga angustirostris*: Stewart 1997) or extreme secondary sexual characters such as the male gharial's bulbous nasal protuberance (Martin and Bellairs 1977). Among extant reptiles, male lizards tend to be physically larger than females, although larger females are known in almost every family. By contrast, snakes and chelonians are almost exclusively biased towards larger females, and in the latter the magnitude in size difference can be striking. Lizards which frequently engage in male combat and territoriality tend to exhibit male-biased sexual size dimorphism. Larger females are associated with a dramatic increase in fecundity in both snakes and chelonians, and as with lizards only those species that engage in male combat tend to have larger sized males (Fitch 1981; Cox et al. 2007). In mammals, the male tends to show a greater degree of dimorphism, especially in groups that employ polygamous mating systems (see Weckerly 1998; Lindenfors et al. 2007); however,

mammals in which the female is larger or more ornate than the male are by no means rare (e.g. Ralls 1976, 1977). Such reverse sexual dimorphism has been argued as a widespread phenomenon among theropod dinosaurs (e.g. Larson 1994, 1997, 1998), but this idea deserves more careful scrutiny and is discussed later.

There have been attempts to evaluate sexual dimorphism in extinct taxa with perhaps the best known being that of Bennett's (1992) study of *Pteranodon*. Two distinct morphs were described: one physically larger with a distinctive crest, and the other smaller form with a reduced crest. Similar dimorphic crest patterns have been demonstrated in the genera *Pterodactylus*, *Germanodactylus*, *Lonchodectes*, *Anhangura*, *Coloborhynchus* and *Nyctosaurus* (see Unwin 2006). Bennett (1992) noted that while the larger morph of *Pteranodon* was found to exhibit a small and narrow pelvis, that of the smaller morph was larger and deeper; apparently an ideal configuration for the larger pelvic canal required for oviposition. It was thus suggested that the smaller sized morph represented the female. A recent analysis of alligator morphology by Prieto-Marquez et al. (2007) demonstrated that females have deeper pelvic canals than males, though there is much overlap between the genders. This would appear to buttress the argument for dimorphism in *Pteranodon*, though the authors warned of the explicit need for large sample sizes and expressed concerns over Bennett's lack of an extant comparative model to better support his hypothesis.

Both possible and demonstrative examples of sexual dimorphism among extinct and extant archosaurs are summarised in detail.

2.1.1 Crocodilia

Sexual dimorphism is ubiquitous in the crocodilia with males often dramatically larger than females (e.g. Steel 1989; Trutneau and Sommerlad 2006), while in gharials (*Gavialis gangeticus*) the male is not only larger and heavier but sports a nasal flare or 'ghara', a unique structure lacking in the female which appears to be used in visual displays (Martin and Bellairs 1977). However, in some smaller species such as the dwarf crocodile (*Osteolaemus tetraspis*) and the Chinese Alligator (*Alligator sinensis*), females may boast a slightly larger body size and the presence of larger males appears to be correlated with intraspecific male aggression (Cox et al. 2007). There are no reports of dimorphism from the fossil record of crocodilia, an observation likely due to the very small sample sizes available for study, though it is not unreasonable to assume that some extinct crocodilians were dimorphic.

2.1.2 Aves

Extant birds frequently demonstrate sexually dimorphic characters with males exhibiting larger body sizes, more

elaborate colour, exaggerated ornamentation and specialised plumage (e.g. Amadon 1975; Price and Birch 1996; Szekely et al. 2007). Similar observations have been made in extinct avian species, with the confuciusornithid *Confuciusornis sanctus* of the Early Cretaceous of China found to have two apparently distinct morphs, where the presumed male bears extended twin-tail feathers (Hou et al. 1995) similar to those of modern avians (e.g. Andersson 1982). There are, however, several extant avian groups where dimorphism is reversed; as an example, females of the Falconiformes and Strigiformes are noticeably larger than males (Amadon 1975; Smith 1982; Kruger 2005). Reversed sexual dimorphism (RSD) among predatory birds tends to increase dramatically with the proportion of birds included in the diet (Andersson and Norberg 1981). It should be noted that although sexual dimorphism in extant birds is traditionally associated with differences in mating systems, the varying expressions of dimorphism in birds do not always correlate with mating system [see Owens and Hartley (1998) for a detailed discussion]. Analyses of skeletal differences in the sexually dimorphic California Gull (*Larus californicus*) found that the larger males had correspondingly wider synsacra than the females (Schnell et al. 1985).

2.1.3 Sauropodomorpha

Evidence of dimorphism in prosauropods has been well documented in the late Triassic *Thecodontosaurus antiquus*, with 'robust' and 'gracile' forms distinguished by differences in the scapula, humerus, tibia and femur. A perhaps interesting note is that the robust form appears far less frequently than the gracile (Galton 1997; Benton et al. 2000; see also Klein 2004). Similar observations have been reported in *Melanorosaurus readi* (Heerden and Galton 1997) and in *Sellosaurus gracilis*. Galton (1999) concluded that skeletal morphs with a stronger pelvis and three sacral vertebrae represented the female, while morphs with a weaker pelvis and two sacral vertebrae were male. Perhaps the best indication of gender morphs was found as a result of a detailed morphometric evaluation of *Plateosaurus longiceps* by Weishampel and Chapman (1990) who documented subtle variation in femoral dimensions interpreted as structural adaptations to more effectively distribute differing body weights. Based upon careful evaluation of the histology of ontogenetic stages of sauropod long bones, Klein and Sander (2008) reported two very distinct morphotypes in *Camarasaurus*, one small and one large, and suggested that this represented either two separate species or sexual dimorphism.

Dimorphism is rather difficult to ascertain in sauropods as most taxa tend to be represented by single specimens based on incomplete and frequently headless skeletons (Chapman et al. 1997). Despite this limitation, individuals of the Jurassic sauropods *Apatosaurus*, *Diplodocus* and

Camarasaurus were found to demonstrate fusion of the caudal vertebrae (Rothschild and Berman 1991). Explanations based on structural support to allow for either the assumption of a tripod stance or use of the tail as an anti-predator defence were found to be without merit as the phenomenon was not ubiquitous in its distribution (see also Rothschild and Molnar 2005). Only 50% of both the *Apatosaurus* and *Diplodocus* and 25% of the *Camarasaurus* specimens examined were found to exhibit caudal vertebrae fusion. The phenomenon was thus suggested to be sexually dimorphic with the adaptation limited to one sex. It has been suggested that males may have employed the tail in a 'whip-lash' manner as either an intraspecific signalling or combat device or, perhaps, more likely considering the mechanics of reproduction in such massive animals, the modification allowed for an upward and sideways arching movement of the female's tail to allow for effective copulation (Rothschild and Berman 1991; Rothschild and Tanke 1991; Rothschild 1994).

2.1.4 Theropoda

In recent years, there have been several attempts to demonstrate the presence of sexual dimorphism in theropods. These have focused on three particular lines of investigation: (1) the possibility of two distinct morphs in a given taxon, (2) the alleged gender-specific role of the first caudal chevron and (3) the putative role of hornlets and crests on certain regions of the skull of some taxa. What follows is a detailed summary and critical review of these concepts and hypotheses. Alleged occurrences of 'gracile' and 'robust' forms have been described for *Coelophysis bauri* (Colbert 1990), *Syntarsus rhodesiensis* (Raath 1990) and *Tyrannosaurus rex* (Carpenter 1990a; Larson 1994).

The Ghost Ranch dinosaur quarry in New Mexico has yielded at least 1000 individual specimens of the Upper Triassic theropod *C. bauri* and is considered the most detailed and complete monospecific assemblage known (Schwartz and Gillette 1994). Colbert (1989, 1990) found two distinct morphs among the specimens, one with a lengthened skull, a long neck, small forelimbs and fused sacral spines, while the other had a shortened skull, a shorter neck, larger forelimbs and free sacral spines. Colbert (1990) suggested that the differences were due to sexual dimorphism though remained uncertain as to which possible morph represented which gender. However, using a principal components analysis, Covey (1993) argued that there was no separation into dimorphic groups, with changes in hindlimb proportions due to ontogenetic change which may reflect age-related changes in locomotion.

While evaluating specimens of *Syntarsus rhodesiensis* collected from a monospecific fossil bed of individuals of differing size classes, Raath (1990) reported consistent variation among certain skeletal elements, in particular the

trochanters and muscle attachment scars of the femur. Plotting the transverse width of the lesser trochanter against the maximum width of the femoral head yielded three distinct clusters, two of which demonstrate small values for the width of the trochanter and one that is noticeably robust (see Chapman et al. 1997). Raath (1990) interpreted these two small clusters as being juveniles and mature males, with sexual maturity estimated to occur when the width of the femoral head attained 28 mm. While Colbert (1990) remained cautious in regard to assigning a specific gender to his *Coelophysis* morphs, in stark contrast, Raath speculated that the more muscular 'robust' form was most likely female because (1) the specimens had apparently been killed in a sudden catastrophic event and that females would be more likely to remain with their young, (2) a skewed sex ratio with 'juveniles' and 'robust' females outnumbering 'gracile' males may indicate the maintenance of a harem by a dominant male or males and (3) should the assemblage represent a normal *Syntarsus* population distribution, a highly skewed sex ratio biased towards females would tend to greatly increase their reproductive efficiency.

In regard to the argument that the assemblage included mothers reluctant to abandon the young, this would appear to be supported by discoveries of *Oviraptor mongoliensis* associated with a nest (see Norell et al. 1995; Dong and Currie 1996; Clark et al. 1999). However, this interpretation is confounded, as in each case, it is not known whether the attending adult was male or female. The idea that *Syntarsus* males maintained harems is problematic for in all extant harem-keeping tetrapods, males are noticeably larger than females due to the ensuing competition among males to secure breeding access (Grier and Burk 1992). Furthermore, there are no records that describe resource defence polygyny being associated with RSD. The third point pertaining to whether the assemblage was representative of *Syntarsus* remains contentious as the alleged sex ratio may have been a result of sampling bias, a possibility that Raath (1990) recognised. During a histological evaluation of *Syntarsus* femora of variable ontogenetic stages, Chinsamy (1990) noted that large perimedullary cavities were found only in specimens assigned to the 'robust' morph, suggesting a direct link to an increase in both phosphate and calcium requirements during reproduction (see also Schweitzer et al. 2005a). Since the phenomenon is known to be directly correlated with egg production in extant avians (Meister 1951), Chinsamy thus postulated that the robust morph was female, though as a caveat, she conceded that the bone erosion may have been due to other circumstances. It is worth noting that in a study evaluating *Syntarsus kayentakatae*, Rowe (1989) concluded that there were possibly two sexual morphs based on the development of muscle attachment points. It is therefore concluded that while *Syntarsus rhodesiensis* was most likely dimorphic,

it is not currently possible to conclusively differentiate which morph represented which gender.

There have been references made to possible 'gracile' and 'robust' forms in the troodontid *Saurornithoides*, though there do not appear to be any detailed accounts (see Larson 1994; Molnar 2005). A study of *Dilophosaurus* by Gay (2005) found no indication of dimorphism in the postcranial elements, though sample sizes were considered too small to allow for a reliable analysis of the cranial crests which, considering their likely role in sexual display and species recognition, may have shown variation between the sexes. Thulborn (1994) noted variation in the proportions of both the premaxilla and maxilla of *Allosaurus fragilis* and described 'gracile' types having 16 to 17 maxillary teeth and 'robust' forms with 14 to 15, a difference interpreted as possible sexual dimorphism. During a morphometric analysis of *Allosaurus*, Smith (1998) found that both the dentary and weight-bearing elements formed a bimodal distribution to which he suggested a possible sexual difference, though no assignment was made between morph and gender as this was considered too arbitrary. Studies on *Allosaurus* pelvic elements from the Cleveland Lloyd Dinosaur Quarry near Price, Utah, USA found that approximately half of the adult individuals had pubes that were unfused distally. As many extant vertebrates produce hormones that cause their pelvic ligamentous tissues to soften to allow for easier passage of eggs, this was interpreted as a possible sexual character (after Madsen 1976).

Dimorphic variation has been reported in the pelvis of *T. rex* with Carpenter (1990a) noting that the angle between the caudal vertebrae and the ischia was a few degrees greater in the 'robust' morph than in the 'gracile' morph. While suggesting a similar dimorphism based on possible variation in the humerus and postorbital bones, Larson (1994) corroborated the differences in the ischium and sacrum. Both authors concluded that the phenomenon was an adaptation allowing for more efficient passage of eggs during oviposition and that the 'robust' morph was therefore female. This interpretation was questioned by Prieto-Marquez et al. (2007) based on the lack of an extant comparative model and the absence of a quantified degree value for the ischial angle. Larson (2002) further described the 'robust' specimens as having wider hips, which was considered an adaptation for oviposition and thus confirmation of the morph's female gender. These conclusions were questioned by Brochu (2002), in that any alleged variation was far more likely to be based on ontogenetic and temporal factors. With reference to professed gender differences in the pelvis, Brochu (2002) observed that at the time 'hip-related sexual dimorphism has not been demonstrated in any egg-laying amniote'. This was echoed by studies of alligator anatomy which found no significant statistical support for gender assignment using pelvic osteological correlates (e.g. Prieto-

Marquez et al. 2005; Gignac et al. 2006). In the follow-up work, Prieto-Marquez et al. (2007) reported weak evidence for sexual dimorphism in the proportions of the alligator pelvic canal, with females seeming to have slightly deeper pelvic canals (see above). However, there was a tremendous overlap between the sexes, hence the need for large sample sizes, a situation frequently unobtainable for dinosaur material. Further caution in regard to the use of crocodylians for sexing extinct archosaurs was raised by Bonnan et al. (2008) who demonstrated that size and individual variation have more influence on male and female alligator femoral shape than on gender. Further confounds are introduced by differences between the genders in reproductive physiology (e.g. bone massing for shell formation in reproductively active females), differences in locomotion gait between crocodylians and dinosaurs, variation in sexual size dimorphism and as with the aforementioned studies the need for very large sample sizes.

It is important to recognise that the dimorphism previously suggested in *C. bauri* and *Syntarsus rhodesiensis* described variation in the skeleton and not actual physical size. The argument put forward by Larson (1994) was that the alleged 'female' *T. rex* morph was substantially larger than the male and that RSD was a standard model for theropod dinosaurs. Larson's arguments for theropod RSD were based in part upon early work by Amadon (1975) who suggested that the key to understanding RSD in extant avian birds of prey (e.g. Falconiformes and Strigiformes) was the monogamous relationship between male and female. No competition for access to females and a one-to-one sex ratio meant that there is no need for males to be larger and that a larger female would benefit from increased reproductive potential (e.g. Larson 1994, 1998). The problem with using birds of prey as an analogue for theropod dinosaurs is that the former are mostly arboreal while the latter are terrestrial. Andersson and Norberg (1981) were able to demonstrate conclusively that sexual dimorphism in birds of prey increases with the proportion of birds being preyed upon and therefore sexual size differences among these predators are directly related to the pursuit and capture of other birds in flight, with the smaller male capable of superior speed and agility. A larger female and smaller male thus engage in resource partitioning, able to select and capture different size classes of flying avian prey and thus increase their hunting efficiency. This observation was also noted by the work of Paton et al. (1994) and alluded to by both Brochu (2002) and Molnar (2005) in their own evaluations. It is easy to see why this explanation for RSD has no relevance for terrestrial theropods and in that respect it is not a valid model.

The matter of dimorphism in *T. rex* serves as a timely introduction to a possible gender-specific role of the first caudal chevron as it was in this species that the

phenomenon was first noted. The hypothesis was originally suggested by Romer (1956, p. 267; but see also Nopcsa 1929) who suggested that the first haemal arch in crocodile skeletons appeared to demonstrate positional variation between male and female specimens, though unfortunately no data were presented to allow verification. This observation was followed up by Larson and Frey (1992), who reported that serial dissections of extant crocodilians apparently verified this dichotomy. The theory was formally presented by Larson (1994) who purported that the phallus of male crocodilians, an organ which retracts when not in use, was found to attach to the first haemal arch via a 'penis-retractor muscle'. As such in males the first haemal arch is more or less the same size as the second, an adaptation thought to yield greater attachment surface area for the retractor muscle and, in direct contrast, the first arch of females is approximately one half the size of the second. It is further suspected that this smaller arch can act to allow for easier passage of eggs during oviposition (see also Horner and Lessem 1993; Larson 1994, 1998; Powell 2000). An alleged positional variation in chevrons has apparently been reported for the troodontid *Saurornithoides*, but to date no visual documentation has been published (see Larson 1994).

Haemal arch geometry would appear to offer potential for gender identification in dinosaurs, though unfortunately recent investigations suggest otherwise. After evaluating the skeleton of the tyrannosaur colloquially known as 'Sue', itself an alleged female based on haemal arch anatomy, Brochu (2002) was unable to identify the differences alleged by Larson (1994, 1998) and concluded that any discrepancies were more likely due to factors such as individual, ontogenetic and temporal variation. A more detailed investigation undertaken by Erickson et al. (2005) tested the haemal arch theory in a series of experiments (see also Prieto-Marquez et al. 2005; Gignac et al. 2006). In regard to claims of 'penis retractor muscles', it was stressed that no such putative structure appears to exist, with the relevant musculature (the *mm. transversus laterales pars dorsalis* and *ventralis*) present in both crocodilian sexes where they appear to function in both pulling the vent caudally and in closing it with any potential role in penile movement unknown. The skeletons of several dozen alligators, ranging from juvenile to adult and for which gender was known, were evaluated for any evidence of first chevron variance. Then a number of skeletonised museum specimens representing a variety of extant crocodilian species were subject to a similar examination. In both cases, no correlation was found between either the relative position or length of the first haemal arches and gender. A further examination of preserved alligator embryos found that chevron chondrogenesis is complete at the stage when the embryo is still sexless. As the gender of crocodilians is based upon incubation temperature (e.g. Deeming and Ferguson

1989), this observation alone renders the haemal arch theory untenable.

Another suggested indicator of theropod gender is the presence of hornlets and other cranial ornamentation features of which appear to be fairly common in this group. Past theories regarding these structures have included use as offensive and defensive weapons (e.g. Bakker 1986) and species-specific signalling devices to elicit successful courtship and reproduction (e.g. Molnar 1977). The idea that cranial ornaments may have served a significant function as signals has been advanced by Molnar (2005) who argues this as the most parsimonious explanation. Hornlets, crests, rugosities and possible support structures for unpreserved soft tissue extensions could have yielded ideal visual signals pertaining to the bearer's fitness (see also Zahavi et al. 1997). Unfortunately the quality of available material and minimal sample sizes make it difficult to ascertain whether these physical attributes were correlated with only one specific gender or the other, though based on extant models and current female choice theories, it can reasonably be expected that males would have been the more ornate [e.g. see Alcock (1989), Gould and Gould (1989), Grier and Burk (1992) and Andersson (1994) for more detailed discussions].

2.1.5 Ankylosaurs

There is very little information regarding possible dimorphism in ankylosaurs, though Carpenter (1990b) proposed that apparent variation in both the length of the snout in *Panoplosaurus* and the armour layout of *Edmontonia rugosidens* may represent gender differences. Gangloff (1995) further noted the possible dimorphic nature of cranial proportions and dermal plate patterns, but noted that some variation may be due to factors such as ageing or even crushing. Tail clubs would appear to hold promise should they have served a purpose in either male combat or as a sexual display, but variation in this structure in regard to sexual dimorphism was repudiated by Coombs (1995).

2.1.6 Stegosaurus

The function of the unique dorsal plate and ornamentation arrangements of stegosaurs have long been a source of contention. Early ideas advocated that the plates served as forced convection heat loss fins (Farlow et al. 1976; de Buffrenil et al. 1984), though recent histological work has concluded that these structures were associated with primarily the identification of individual species and perhaps secondarily with inter- and intraspecific display (Main et al. 2005). Should the latter suggestion be proven, it can be assumed that there is the distinct possibility of dimorphic trends though no supporting evidence has been reported.

There appears to be dimorphism in the number of sacral ribs in *Kentrosaurus aethiopicus* (Galton 1982a, 1982b) with the extra sacral ribs interpreted as a female trait (Galton 1999). Similar observations have also been recorded in both *Dacentrurus armatus* (Galton 1991) and *Stegosaurus stenops* (Ostrom and McIntosh 1966). In *Lexovisaurus durobrevis*, the parasacral spines are either protracted with a large base or shortened with a comparatively smaller base, a characteristic that has been interpreted as a candidate for sexual dimorphism (Galton 1985, 1990). However, it is unclear as to how these structures could be used to determine gender. The elements were among a large number of disarticulated bones from two or three incomplete specimens and furthermore there are no data regarding where the aforementioned spines might have attached.

2.1.7 Ornithopods

Heterodontosaurids have a pair of caniniform teeth that Steel (1969) and Molnar (1977) suggested might be utilised for either intraspecific combat or social display, as these specialised teeth are thought to be exclusive to sexually mature males. Thulborn (1974) further postulated a gender recognition role or social badge display, while Molnar (1977) noted that adaptations to the jugal bar may have allowed for more substantial biting pressure; for example, holding an opponent male's jaw during combat. The first digit of iguanodontids serves as a 'spike' and may have been used as either or both a defensive weapon or as a means of breaking open seeds and fruit, though there appears to be no evidence that the structure was exclusive to one gender (see Norman 2004). There does not appear to be any reliable evidence of confirmed sexual dimorphs in this particular group.

Hadrosaurids are arguably among the best known of all the Dinosauria with extensive material collected regarding their skeletal anatomy, eggs, hatchlings, juveniles and taphonomy (e.g. Horner et al. 2004). This diverse group is known for a wide variety of crests and cranial structures and would appear to be ideal candidates for detecting sexual dimorphism (e.g. Hopson 1972, 1975; Chapman and Brett-Surman 1990).

Dodson (1975) evaluated cranial crests using bivariate plots and was able to determine what appeared to be male and female morphs in *Corythosaurus casuarius*, *Lambeosaurus lambei* and *L. magnicristatus* with the larger crested specimens considered to be males. However, by employing a combination of updated biostratigraphic and GPS data, it has been demonstrated that the different crest morphs of the three genera are not randomly distributed within the strata. Rather, the large crested *Corythosaurus* 'male' morphs are stratigraphically separated from the 'female' morphs. Further confounds to Dodson's original hypothesis are that the large crested morphs of the alleged

'male' *Lambeosaurus* occur in younger strata than in the 'female' variants, and that the high degree of crest variation makes identification of individual specimens difficult (Evans et al. 2006; Stokstad 2006a). It was previously thought that the elongated crest of *Parasaurolophus* was a male character with females having smaller structures (e.g. Hopson 1975), though this interpretation was challenged by Sullivan and Williamson (1999) who pointed out that there was no evidence that the two putative forms co-existed and were likely separate taxa. The only other hadrosaurian taxon for which dimorphism may be present is *Edmontosaurus*, some specimens of which have noticeable circumnarial excavations that may have supported inflatable diverticula (Horner et al. 2004). These may have been exclusive features of male *Edmontosaurus* for sexual display or vocalisation, though this possibility does not appear to be well developed in the literature. It should be noted that some birds such as the greater sage grouse (*Centrocercus urophasianus*) employ inflatable air sacs to modify or accent their vocal displays (e.g. Dantzker and Bradbury 2006).

2.1.8 Marginocephalia

The Pachycephalosauria are perhaps best known for and characterised by the thickened frontoparietal bones along the roof of the skull (e.g. Goodwin 1990), an adaptation long thought related to intraspecific combat among males during which two rivals would face each other and engage in head-butting bouts similar to the extant bighorn sheep *Ovis canadensis* (Colbert 1955; Galton 1970, 1971; see also Snively and Cox 2008). This interpretation was questioned by Sues (1978), Carpenter (1997) and Goodwin et al. (1998) who raised objections based upon the minimal contact area between the two opposing heads and the lack of a correcting mechanism, favouring instead a flank-butting model as observed in male African antelope (see Leuthold 1977). In this scenario, rival males would stand roughly parallel facing either each other, or in the same direction, and deliver targeted blows to the sides of the body. Studies of skull histology add support that cranial display structures were most probably a key means of intraspecific recognition and communication with sexual display functions secondary (Goodwin and Horner 2004). Any formal consensus regarding pachycephalosaurid agonistic behaviours remains elusive due to differing interpretations of functional arguments and extant models (see Maryanska et al. 2004).

The question of whether sexual dimorphism existed in pachycephalosaurs has long been hindered by overall small sample sizes, which have made such analyses difficult to conduct reliably (Chapman et al. 1997). Brown and Schlaikjer (1943) first suggested the possibility of dimorphs in *Stegoceras* based on two distinct types of dome, suggesting that the presence of a squamosal shelf

may have functioned as a display structure for males, though the caveat was added that the conclusion was purely arbitrary. Goodwin et al. (1998) countered that the squamosal shelf was more likely a characteristic of juveniles and therefore not an indication of gender. The strongest and most robust evidence is offered by Chapman et al. (1981) who undertook a detailed morphometric analysis of *Stegoceras validus* domes. He revealed two distinct morphs: one with a relatively thicker, larger and more convex dome interpreted to represent the male. However, this interpretation was countered by Goodwin (1990) who expressed concerns that no consistent dome measurement technique was employed and further by Goodwin and Horner (2004) who claimed that the study sample was composed primarily of juveniles and subadults. Despite the controversy regarding alleged male and female morphs in *S. validus* domes, Maryanska et al. (2004) concluded that overall the model was robust.

2.1.9 Ceratopsia

The ceratopsids are well known for their cranial ornamentation of bosses, frills and horns, which most likely served primary roles as intraspecific recognition displays (e.g. Farlow and Dodson 1975; Molnar 1977). Sexual dimorphism has been very well documented in terms of both the cranial features and the width and height of the frill in the basal ceratopsid *Protoceratops andrewsi*, with putative males demonstrating a more prominent nasal horn and a wider frill (see Kurzanov 1972; Dodson 1976; Spassov 1979; Chapman 1990; Dodson 1996). A detailed analysis of the postcranial skeleton yielded 19 putative structural differences of the pelvis, abdominal cavity and thoracic vertebra each thought to be directly related to gender (Tereshchenko 2001).

The wide range of variation in the skulls of the more derived ceratopsids has long complicated ideas regarding possible dimorphism (e.g. Dodson 1990; Sampson et al. 1997), though several studies appear to have confirmed its presence. Evaluation of *Chasmosaurus* material strongly suggests that the orientation of supraorbital horncores can be used in determining sexual morphs; the assumption is that the male morph had horncores noticeably more erect and directed vertically from the orbit (Lehman 1990; Godfrey and Holmes 1995). This observation correlates with extant mammals where differences in horncore sizes are known to be associated with sexual dimorphism, in which males tend to have longer or thicker horns (Geist 1966; Packer 1983). Similar observations regarding horncore orientation have been reported for *Pachyrhinosaurus* (Tanke 1988), *Triceratops* (Ostrom and Wellnhofer 1990), *Pentaceratops sternbergii* (Lehman 1993) and for both *Achelousaurus* and *Einiosaurus* (Godfrey and Holmes 1995). Based on analogies with extant vertebrates, Sampson et al. (1997) observed that size-based sexual

dimorphism is likely to be minimal in ceratopsids with horns and frills the most likely candidate for secondary sexual characters. Sampson (1999) discussed the importance of ornamentation in terms of mating signals and subsequent speciation events in ceratopsid populations. However, it should be noted that Sampson (1995a) warned that conclusions regarding putative sexual morphs in this group were confounded by frequent small sample sizes and possible temporal differences, so caution is necessary.

2.1.10 Conclusions

It is surmised that determining the sex of dinosaurians remains an elusive goal with statistical analyses of skeletal material hampered by small sample sizes, preservation bias, temporal issues and ontogenic change (Padian et al. 2005), in addition to modelling problems and intraspecific variation (Powell 1998; Bonnan et al. 2008). However, despite the aforementioned caveats, it is imperative to recognise that both sexual and size dimorphism are widespread phenomena throughout extant vertebrate and invertebrate populations [e.g. see Fairbairn et al. (2007) and chapters within], and there is no logical reason as to why extinct taxa would be exempt. In that respect, there is strong circumstantial evidence of possible sexual dimorphism to be found in most dinosaur groups, but only in the ceratopsians is there any degree of confidence as to which morph might represent which gender, with the more robust and ornate variants most likely male.

One possible line of query remains the previously noted work concerning the alleged presence of medullary tissue in long bones. This highly specialised and structurally unique endochondral bone is formed as a response to released gonadal steroids. It is deposited in the medullary cavities and resorbed during ovulation at which time it serves as a vital mineral store for the production of eggshell and is well documented in extant female birds (e.g. Bloom et al. 1941; Simkiss 1967; Taylor et al. 1971; Dacke et al. 1993; Chinsamy-Turan 2005). Female crocodilians have been demonstrated to break down structural bone and disperse this via circulation during eggshell formation (Elsay and Wink 1985) in a manner similar to that documented in chelonians (e.g. Edgren 1960; Magliola 1984). The formation and presence of medullary bone has not been observed in crocodilians and appears to be a unique physiological phenomenon in extant birds (Elsay and Wink 1986; Schweitzer et al. 2007). The aforementioned apparent discovery of this specialised tissue in a fragment of long bone from a *T. rex* by Schweitzer et al. (2005a) indicates that medullary bone evolved somewhere in the dinosaur–bird lineage after the divergence of the crocodilians. It is not known whether the *Tyrannosaurus* material was extracted from a ‘gracile’ or ‘robust’ form so no correlation could be made between putative medullary bone and alleged sexual morph,

although it should be noted that the presence of size-based dimorphism in this particular species is highly questionable (e.g. Brochu 2002). Possible further evidence of medullary bone has been inferred from the tibia of *A. fragilis* and from the femur and tibia of *Tenontosaurus tilletti*, both of which contain material that appears to be morphologically homologous to that described for *Tyrannosaurus*. Should such an interpretation prove correct, the ability to produce this highly specialised bone took place at least as early as the divergence of the saurischian and ornithischian lineages (Stokstad 2006b; Werning and Lee 2006; Lee and Werning 2008). Furthermore, the apparent lack of medullary tissues in the long bones of oviraptorids associated with nests was considered evidence that the specimens were male and that a paleognath male-only parental care system was employed (Varricchio et al. 2008a).

The potential presence of medullary structures has also been suggested in *Syntarsus rhodesiensis*, though this was reported along with the caution that there may have been other geochemical causes for the apparent phenomenon (Chinsamy 1990). While medullary tissues would appear to hold the answer as to the gender of a particular fossil, there are strong caveats and confounding variables involved. The bone microstructure of dinosaurs is different from that of extant birds, containing an unusual amalgam of both avian and classic reptilian traits; furthermore, basal birds such as the enantiornithines have bone characteristics that tend to differ substantially from their extant relations (e.g. Chinsamy et al. 1994, 1995; Chinsamy and Barrett 1997). Kaye et al. (2006) examined a variety of specimens including *Triceratops*, an ankylosaurid, a hadrosaurid and a champsosaur from both the Lance and Hell Creek formations. Examination of these assorted bones using both a scanning electron microscope and energy dispersive spectroscopy, yielded a variety of structures that were homologous to prior descriptions of *Tyrannosaurus* soft tissue reported by Schweitzer et al. (2005b). More detailed analysis showed structures that appeared to be substantive evidence of soft tissue, were in fact mineral and microbiological in origin whose morphology allowed for multiple interpretations. Similar observations were made for ammonoids and the conclusion was reached that morphology alone is not a reliable method for soft tissue identification. Infrared spectroscopy was utilised to compare fossil bone coatings along with modern collagen and biofilms, the results of which indicated that the fossilised specimens demonstrated a more significant match to modern biofilms than collagen (Kaye et al. 2007; Kaye and Gaugler 2008), and subsequent carbon dating of the aforementioned biofilms strongly suggest a modern origin (Kaye et al. 2008). It is clear that positive identification of specialised bone structures is problematic and even proponents of medullary bone have admitted that, despite the extinct and extant taxa tissues bearing strong

morphological homology, whether homology extends to being functional is not testable (Werning and Lee 2006).

There have been attempts to suggest gender based on the presence of eggs either within or in close proximity to a skeleton. Spherical structures of approximately 10 mm in diameter found scattered near the remains of a *Compsognathus longipes* were originally interpreted as dermal ossifications (von Huene 1901) but were later considered immature eggs (Griffiths 1993). A well preserved *Sinosauropteryx prima* was found with an internal pair of eggs positioned low in the abdomen anterior to and above the pubic boot, though the authors did suggest the possible presence of more (Chen et al. 1998). These were of a much larger size (37 × 26 mm) than the purported eggs from *Compsognathus* which is considered to be closely related to *Sinosauropteryx*, an observation that raises further doubts as to Griffiths's (1993) conclusion. The recent report of an oviraptorid skeleton containing a pair of fossilised eggs (Sato et al. 2005) is the only unequivocal verification of a dinosaurian fossil's gender and would appear to be an ideal candidate for medullary tissue testing to confirm the possible usefulness of this utility. Unfortunately, to date the 'shelled egg' oviraptorid remains known from only a very brief description and at this time has not yet been evaluated for any evidence of medullary tissues (Dr Yen-nien Cheng, personal communication).

2.2 Evidence for courtship, antagonistic behaviour and social structure

The formation of a temporary, seasonal or extended pair bond between a male and a female for reproduction involves an exchange of signals. The classic ethological explanations of such courtship (or pre-copulatory) behaviour tended to focus on four main types of functions:

- (1) *Gender- and species-specific recognition.* Individuals ensure they are dealing with the opposite gender of the same species.
- (2) *Mate attraction and mating orientation.* Widely separated or dispersed males and females are brought together via the use of long-distance sexual signals, while short-range courtship behaviours result in the alignment of male and female during copulation.
- (3) *Synchronisation of mating and parental behaviour.* Courtship stimulates male and female physiology to a similar reproductive state thus ensuring cooperation between the sexes.
- (4) *Overcoming aggression.* Courtship helps to prevent one gender from attacking the other as some taxa are often highly aggressive towards conspecifics during the breeding season.

Animals can attract the attention of a potential mate by either engaging in direct physical combat or relying upon

visual displays. The end result is that there tends to be strong selection pressure towards the development of characteristics, such as offensive weapons or exaggerated physical features that act to enhance or refine an individual's chances of successfully mating. Selection pressures brought about by competition for potential mates are known as sexual selection (Darwin 1871). More recent interpretations of courtship behaviour incorporate many elements of this theory; for example, as an effective means of allowing for comparisons to be made between males of the same species and an evaluation of the quality of their genes (e.g. colour, size and ornamentation). The two views are not in conflict, but rather represent differences between proximate and ultimate explanations of behaviour (after Grier and Burk 1992; see also Kodric-Brown and Brown 1984; Gould and Gould 1989). There have been numerous enhancements and criticisms of this theory (e.g. Roughgarden et al. 2006; see response by Dall et al. 2006), though a detailed analysis is beyond the scope of this investigation and as such a basic overview will suffice.

This evolutionary phenomenon has two distinct variations. The most common form of sexual selection is intersexual selection, more commonly referred to as 'female choice'. This variant occurs when males compete with each other to be chosen by females and is considered to be both the most common expression of sexual selection and the reason for the often dramatic secondary sexual characters (e.g. Kirkpatrick 1982; Alcock 1989; Hill 1990; Grier and Burk 1992; Barnard 2004). There are several theories concerning the mechanisms of female choice. Runaway sexual selection (colloquially referred to as the 'sexy son' theory) postulates that exaggerated male characteristics such as bright colouration, long tail feathers or physical ornamentation can evolve through a process in which the particular male trait and the female's preference for that trait become linked at the genetic level. It is important to note that the trait in question simply needs to be attractive to females and does not have to benefit the male in any way. The end result is that when males with the desirable trait copulate with females with a preference for the trait, both the trait and its preference are inherited by their male and female offspring. The 'runaway' factor refers to the mechanism by which the positive feedback loop of increasingly exaggerated male traits and increasingly strong female preference, causes the male trait to become more and more extreme over the progress of time. This phenomenon continues until acted upon by natural selection in that once the overall cost of the trait outweighs survival benefits, the process comes to a halt (see Fisher 1915, 1930, 1958). On a related note, the 'Handicap Principle' suggests that any sexually selected trait that tends to be costly to a male can act as a signal of genetic quality because only males in pristine physical condition could afford to maintain it (Zahavi 1975, 1977; see also Kodric-Brown and Brown 1984).

Intrasexual selection is especially prevalent among males and tends to express itself via fighting or displays, resulting in greater body size, gender differences in colour, protective armour and aggressive weaponry. However, care must be taken when identifying putative characters as dimorphism because they can have other causes such as differences in growth rates or feeding strategies. This form of selection can also occur at the post-copulatory stage when sperm compete internally to fertilise eggs and there are a variety of strategies males employ to increase their chances at successful fertilisation. These include pre-copulatory mate guarding, the depositing of plugs in the female reproductive tract and the use of structures on the penis to displace sperm from prior matings (e.g. Alcock 1989; Grier and Burk 1992; Barnard 2004). Females can also employ similar tactics such as cryptic female choice in which they discard a male's sperm without his knowledge (Eberhard 1990, 1996).

The complicated nature of pre-copulatory behaviour does not easily reveal itself in the fossil record, so any discussion ultimately tends to rely on comparing and contrasting two closely related extant archosaurian taxa, namely, the crocodilians and birds. Crocodilian courtship includes a broad spectrum of activity that includes a variety of vocalisations (e.g. Campbell 1973; Garrick et al. 1978; Staton 1978), probable olfactory cues (e.g. Reese 1921, 1931) and extensive tactile stimulation (e.g. Kofron 1991; Vliet 2001). A wide range of both visual and percussive displays are employed such as bubbling, jawslaps and exaggerated head, body and tail movements. Threats and combat occur in both sexes: between males for territory or breeding access and between females for choice nesting places (e.g. Pooley and Gans 1976; Garrick and Lang 1977; Lang 1987; Steel 1989; Vliet 1989; Thorbjarnarson and Hernandez 1993). The courtship of avians involves an equally impressive range of signals that incorporate both sophisticated vocal repertoires (e.g. Kroodsma 2004) and a variety of behaviours which run the gamut from courtship feeding (e.g. Lack 1940; Stokes and Williams 1972; Tasker and Mills 1981; Wiggins and Morris 1986; Green and Krebs 1994) and courtship flights (e.g. Bent 1961; Hamerstrom 1986), the construction and maintenance of bowers (e.g. Borgia 1985), an extensive array of visual displays (e.g. Alcock 2004) and exaggerated ornamentation including brightly coloured and elaborate plumes, inflatable throat sacs and tail feather trains (e.g. Andersson 1982; Petrie and Halliday 1994; Alcock 2004). Crocodilians and birds appear to share a common and widespread use of both visual displays and vocalisations to facilitate pairing and the onset of reproductive behaviour. In that respect, the two characters represent a logical starting point for comparisons with dinosaurs.

2.3 Evidence for visual display organs and associated behaviours

Cranial ornamentation and putative display structures in theropods are well documented. Such structures are widespread among ceratosaurs with *Ceratosaurus nasicornis*, *Dilophosaurus wetherilli* and *Syntarsus kayentakatae* all possessing prominent cranial crests. Those of *Dilophosaurus* and *Syntarsus* are considered far too fragile to have served as offensive weapons and were likely used for display purposes only (Tykoski and Rowe 2004). Likewise, the hollow median frontal dome of *Majungasaurus atopus* yielded similar limitations (Sampson et al. 1998). The lacrimal hornlets, median nasal horn and dermal osteoderms of *Ceratosaurus* and the supraorbital horns of *Carnotaurus sastrei* appear more sturdily constructed (Czerkas and Czerkas 1997; Tykoski and Rowe 2004). In that respect, they may have used both during intraspecific combat for resource access or territory and to attract sexual partners or intimidate rivals.

The tetanurans include both the Carnosauria and Coelosauria, two highly diverse groups that tend to be characterised by an enlarged manus with no fourth and fifth digits (Holtz et al. 2004). The lacrimal horns of *A. fragilis* (Madsen 1976), the unique transverse crest of *Cryolophosaurus ellioti* (Hammer and Hickerson 1994; Smith et al. 2007) and the large midline hollow crest of *Monolophosaurus jiangi* (Zhao and Currie 1993) appear to be adapted primarily as interspecific visual signals. There is extensive cranial ornamentation among the tyrannosaurids with ridges and hornlets spread across the nasals, lacrimals, jugals and postorbitals (Bakker 1986; Holtz et al. 2004), which undoubtedly served a social function. While evaluating the cranial osteology of *T. rex*, Molnar (1991) made note that the presence or absence of a horn-like rugosity on the postorbital might be representative of a gender difference, though no claim was made as to which gender might have sported this character. Perhaps the most unique structure among theropods is the elongated spinous processes or neural spines of *Spinosaurus aegyptiacus* and the associated dorsal crest or 'sail' (Dal Sasso et al. 2005). It has long been thought that the structure served as a heat dissipation mechanism, though Bailey (1997) argued that instead of 'sails', the long spines would have supported for energy storage similar to those seen in extant 'hump-backed' mammals such as bison, in addition to a possible heat exchange function. Bailey argued that the spinous processes of *Spinosaurus* vertebrae are similar in appearance to those of bison in being flattened and cranio-caudally elongate rather than the simple thin cylinder structure of basal synapsids such as *Dimetrodon* or *Edaphosaurus*. However, this theory was challenged by Holtz et al. (2004) who demonstrated that the basal condition for the dorsal spinous process of theropods is rectangular rather than cylindrical, and that the structures

observed in *Spinosaurus* are a simple exaggeration of this ancestral condition. While a putative thermoregulatory function cannot be effectively ruled out, it is more parsimonious to propose a social role for the 'sail' which could have been utilised in lateral displays during courtship behaviour and intraspecific interactions or for taxon recognition.

Courtship behaviour and other social interactions of extant birds frequently employ the use of colourful, ornate and exaggerated feathers for display (e.g. Alcock 2004). Over the past decade a variety of small theropod dinosaurs have been found preserved with integument. Some of these structures were basic downy filaments and have been described in numerous theropod groups including the compsognathids *S. prima* (Ji and Ji 1996; Chen et al. 1998; Currie and Chen 2001) and *Sinocalliopteryx gigas* (Ji et al. 2007), the therizinosaurid *Beipiaosaurus inexpectus* (Xu et al. 1999a), the tyrannosaurid *Dilong paradoxus* (Xu et al. 2004) and the dromaeosaurid *Sinornithosaurus millenii* (Xu et al. 1999b; Ji et al. 2001). Modern feather structures are well documented in *Archaeopteryx lithographica* (e.g. Christiansen and Bonde 2004; Wellnhofer 2004) and in recent years several other small theropods have been found to have this feature. *Protarchaeopteryx robusta* has a row of symmetrical feathers on both arms in addition to a series of feathers extending from a rather short tail (Ji and Ji 1997; Ji et al. 1998). A similar integument was described for the oviraptorid *Caudipteryx* (Ji et al. 1998) and the troodontid *Jinfengopteryx elegans* boasted a covering of pennaceous feather impressions (Ji et al. 2005; Xu and Norell 2006). The two dromaeosaurids *Microraptor zhaoianus* (Xu et al. 2000) and *Cryptovolans pauli* (Czerkas et al. 2002; Norell et al. 2002) were unique in having long apparent flight feathers on both their forelimbs and hindlegs. The proximate and ultimate function of these structures have proven to be controversial (e.g. Sues 2001), though there can be little doubt that they served in courtship and intraspecific displays. The four very long ribbon-like tail feathers described in *Epidexipteryx hui* (Zhang et al. 2008) undoubtedly served in social displays and may have been dimorphic much like the elongate twin tail feathers of the Mesozoic bird *C. sanctus* (Hou et al. 1995, 1996; Ji et al. 1999), though in the case of the latter, sexual dimorphism can only be suggested, as the hypothesis has not been subject to statistical evaluation, nor is there any documentation of further skeletal dimorphic characters.

Recent investigations yield further strength to a social function for the varied display ornaments described in theropods. Tanke and Currie (1998) documented several examples of cranial and facial injuries that had been inflicted by the teeth of conspecifics in *Sinraptor dongi*, *Gorgosaurus libratus*, *Daspletosaurus torosus*, *Tarbo-saurus bataar* and *M. jiangi*. Such aggressive interactions had been previously postulated by Molnar (1991) and

Abler (1992), while a variety of systemic injuries were detailed in *A. fragilis*, some of which were possibly the result of conflict with conspecifics (Hanna 2002). There are numerous accounts of injuries in theropods [see Molnar (2001) for a detailed review] and it is suggested that the most likely causes of at least some of these pathologies were conflicts over food resources and territory (Tanke and Currie 1998; Molnar 2001), though socio-sexual reasons cannot be completely ruled out. Of note are similar injuries described in extinct crocodylians (e.g. Buffetaut 1983). Physical combat between extant male crocodylians is well documented (e.g. Modha 1967; Garrick and Lang 1977; Kofron 1991), the results of which are often severe injuries, including damage similar to that reported in theropods (e.g. Webb and Messel 1977; Brazaitis 1981; Webb and Manolis 1989).

The ceratopsians are perhaps best known for their impressive range of skull shapes which boast an array of neck frills and horn configurations (see Lull 1933; Dodson et al. 2004; You and Dodson 2004). Earlier literature concluded that the primary function of these diverse structures was to serve as an anti-predator defence (e.g. Hatcher et al. 1907; Lull 1933; Colbert 1948, 1961). However, the remarkable range in diversity of these structures coupled with the often rather thin, well-vascularised nature of the frills made this particular theory highly improbable (Dodson et al. 2004). Behavioural comparisons with extant ungulates have yielded a more complete picture. Geist (1966) undertook a detailed evaluation analysing the evolution of horn-like organs in ungulates and noted the ubiquitous trend towards cephalisation of display structures, concluding that interspecific conflict is an unlikely driving force in the evolution of horns. Rather, it is intraspecific antagonistic contact among rutting males to achieve dominance, intimidating potential rival males and defending discrete territories that present a more potent influence.

The evolution of horns appeared to incorporate several distinct evolutionary phases, the first of which involved broadside display and combat. In this initial phase, small sharp horns are swung laterally against the flanks of an opponent to inflict pain or discomfort. Examples of this combat mode are the North American mountain goat (*Oreamnos americanus*), chamois (*Rupicapra* spp.) and giraffe (*Giraffa camelopardalis*). Clearly, there would be a selective advantage to neutralising these offensive weapons which is seen in the second phase. Large strong horns are arranged in a full frontal display to catch an opponent's horns thus countering the destructive power of the preceding blow. Contests among males are therefore based upon shoving and wrestling bouts as observed in bison (*Bos bison*), wild cattle (*Bos* spp.) and African elephants (*Loxodonta* spp.). It is not unusual for horns to be covered with elaborate spirals, bumps and ridges that act to both 'bind' the opponents together during a bout and

guard against an attack on the flank. Among males that employ second phase horn layouts, combat can be further divided into two distinct variants:

- (1) *Frontal ramming*. Opponents rush towards each other to deliver a heavy head-on blow, a behaviour common to musk ox (*Ovibos moschatus*), muflon (*Ovis musimon*) and Dall Sheep (*Ovis dalli*).
- (2) *Frontal pushing*. Opponents lock their horns together and proceed to push and wrestle with one another, a tactic commonly observed in male African antelopes, gazelles and cervids. Species in this particular group are the most likely to boast ridged and spiralled horns that facilitate a 'locking together' of the contestants (after Geist 1966).

Similar behaviour has been documented in lizards in which cranial spikes and protrusions are employed during male intraspecific aggression. Adult male marine iguanas (*Amblyrhynchos* spp.) frequently engage in head to head shoving matches and although there are no horns, a series of rugosities on the skull appear to serve a similar purpose (Carpenter 1967). Horned lizard (*Phrynosoma* spp.) males are equipped with occipital spikes, and while physical combat tends to be rare the horns can inflict injury (Lynn 1965; Whitford and Whitford 1973). Perhaps the most striking similarities to ceratopsid dinosaurs are to be witnessed in the cranial ornamentation observed among certain males of the Chameleoniidae. Jackson's chameleon (*Chameleo jacksoni*) males have a triple horn layout, with one rostral and two supraorbital. During combat, males lock their horns together, pushing and wrestling with each other in an attempt to dislodge the opponent from a branch. Injuries can occur when one combatant stabs an unprotected region of the other (Bustard 1958; Rand 1961; Van Mater 1971, Carpenter and Ferguson 1977). One particular drawback with this analogy is that the horns are directed in a horizontal manner, whereas in ceratopsians the horns boast a more antero-dorsal orientation (see Farke 2004).

The use of ungulates as putative behavioural models for extinct forms is not without precedent. Barghusen (1975) was inspired by Geist's hypotheses in his investigations of the cranial structures and skull modifications of late Permian dinocephalians for which he suggested a combat function. Lull (1933) was the first to propose that the horns of ceratopsian dinosaurs could have served a role in agonistic encounters, an argument based upon apparent damage inflicted by the horns to the bony frill. Inspired by the aforementioned work of Valerius Geist (e.g. 1966, 1971, 1972, 1974), a more detailed evaluation by Farlow and Dodson (1975) proposed three distinct putative combat variations. In phase one agonistic encounters, two males stood parallel to each other and used their small nasal horns to deliver blows to the opponent's flank, a strategy suggested for ancestral

ceratopsid species (e.g. *Protoceratops* and *Leptoceratops*). The combat techniques for phases two and three are based on the length of the frill being either short or long. Phase two encounters envision two competing long-frilled males standing face to face whereupon the two opponents locked their horns together and proceeded to shove and wrestle with each other in a test of strength and endurance. This scenario is suggested for long-frilled species (e.g. *Chasmosaurus*, *Pentaceratops* and *Torosaurus*) and the exaggerated height of the frill likely played a substantial social role. In contrast, phase three bouts predict an absence of horn locking as males of short-frilled species (e.g. *Styracosaurus*, *Monoclonius* and *Centrosaurus*) were unable to catch each other's horns. Instead the combatants likely employed their horns to either intimidate or inflict localised injury, a strategy similar to the agonistic encounters in extant rhinoceros (Owen-Smith 1972). It can be noted that *Triceratops* was unusual in being a short-frilled form that likely used a mode of combat similar to that utilised by the long-frilled species. All three phases may have employed their frills as a shield against an opponent's horns, while the horns and the frill likely served both for display and for species-specific recognition (after Farlow and Dodson 1975).

Molnar (1977) noted that in order for the aforementioned horn-locking hypothesis to be feasible, certain cranial features would be expected. These included a firm buttressing of the brow horncores; protection of eyes, ears and adductors; projection of the horns beyond the snout; a stiffening of the cervical vertebral column and possibly evidence of cranial puncture wounds. As all of these features have been accounted for in ceratopsians (e.g. Hatcher et al. 1907; Moodie 1930; Lull 1933; Swinton 1970; Langston 1975; Forster 1996; Rothschild and Tanke 1997), Molnar surmised that horn locking was highly probable. The only other potential problem would be whether or not the horns themselves could tolerate the stresses inflicted during putative combat. Alexander (1989) analysed correlations of body mass versus horn cross-sectional area in *Triceratops* and several horned mammals and suggested that while the horns of *Triceratops* could physically interlock, it was likely they were not strong they enough to sustain the rigours of combat. This interpretation was challenged by Farlow (1990) who demonstrated that the bony cores of *Triceratops* horns yielded a similar cross-sectional area to the tusks of African elephants which males employ for pushing and wrestling during combat.

Farke (2004) used detailed scale models of *Triceratops* skulls to test the feasibility of horn locking and reported three workable positions in which the horns could successfully lock based on orientation of the combatants' skulls. The horns would thus be expected to inflict specific damage corresponding with pathologies described in the frill (e.g. Hatcher et al. 1907), jugals (e.g. Erickson 1966)

and postorbital horncore tips (e.g. Gilmore 1919). Despite the apparent positive outcome of the experiment, Farke (2004) cautioned that traumatic injuries have not been conclusively demonstrated and suggested more detailed evaluations of available specimens to ensure that any cranial anomaly purported to be inflicted by horns was not due to disease, attempted predation or other environmental factors. There are further possible confounds which must be considered. The probable presence of a keratinous sheath (e.g. Happ and Morrow 2000), which may act to alter both the shape and length of the horn itself, renders proposed fighting positions invalid. Farke (2004) further noted the differences in horn locking between *Triceratops* and bovine mammals. Despite having a similar gross morphology (horns paired, unbranched, posterior location on the skull), the orientation of the horns is quite different. The postorbital horns in most chasmosaurines are directed rostro-dorsally relative to the rest of the skull with only a minor lateral component, whereas those of bovines may direct in a lateral, caudal and rostral orientation (see Farlow 1990).

Furthermore, there is no direct correlation between horn orientation and combat technique, although overall horn shape and length are positively correlated with fighting style in bovines (Lundrigan 1996); however, the combat behaviours and physical positioning employed are either not possible in ceratopsians or would have been undertaken in a very different manner. While the use of horns in combat may well have occurred, it is difficult to make direct explicit comparisons with bovines due to the distinctive horn orientation of ceratopsids and the presence of unique cranial features such as frills and nasal horns (after Farke 2004). Despite these problems, it can be reasonably concluded that species-specific recognition, mating signal displays and intraspecific competition were the most parsimonious functions of the ceratopsid horn and frill layout (e.g. see Sampson 1997b, 1999, 2001; Sampson and Forster 2001). Similarly, Horner and Goodwin (2008) postulated that cranial epi-ossifications documented in *Triceratops* were ornaments that could have been used in conjunction with the forward-directed horns and wide frill to yield an enhanced visual display. Farke et al. (2009) examined the incident rate of lesions on the nasal, jugal, squamosal and parietal bones for both *Triceratops* and *Centrosaurus* and found that the only significant difference was the frequency of damage to the squamosal bone of the frill. It was thus argued that the lower lesion rates for *Centrosaurus* suggested a bias towards either combat directed towards the flanks or the use of cranial ornaments for visual display. In contrast, it would appear that *Triceratops* employed its horns for combat and frill for defence. While skin patterns and colour are unlikely to be fossilised, it can be speculated that the wide area and visual orientation of the frill may

have boasted colourful patterns that intensified during the breeding season.

A specimen of the ancestral ceratopsid *Psittacosaurus* was found with what appeared to be an integument composed of structures resembling the quills of a porcupine. There had been considerable political controversy surrounding this specimen as at one point it had been distributed among a series of private fossil dealers in Europe, thus making independent verification of the claim untestable (Dalton 2001a, 2001b; Stokstad 2001), though at least one early report (Buffetaut 2001) appeared to confirm its legitimacy. A more detailed investigation by Mayr et al. (2002) authenticated the presence of about 100 hollow cylindrical bristles along the dorsal surface of the tail, with each structure approximately 16 cm in length, 1 mm wide at the base and tapered to a point at the tip (Figure 1). Similar structures have been reported for the Asian heterodontosaurid *Tianyulong confuciusi* with a filamentous integument located below the neck and along the back with the largest patch above the tail. These parallel filaments are unbranched, hollow and up to 60 mm in length (Zheng et al. 2009). There is the possibility that the bristles are highly modified scales as seen in the Triassic diapsid reptile *Longisquama insignis* (Reisz and Sues 2000; see also Voigt et al. 2008) and it is not thought that these structures are related to the integuments described for theropods, though, pending future analyses, little more can be speculated. Nonetheless, these discoveries conclusively demonstrate that the types and distributions of integumentary structures among the Dinosauria may well have been highly varied and thus difficult to predict.

Cranial display structures are widespread among the ornithischian dinosaurs. The prominent caniniform teeth and jugal boss seen in heterodontosaurids may have performed important roles in both courtship displays and

social ranking among males (e.g. Steel 1969; Thulborn 1974). Similar display behaviours have been observed in the extant mammalian families Tragulidae and Suidae, which Molnar (1977) considered to be analogous. Among the Iguanodontia, the first manual digit is specialised in the form of a spiked, stiletto-like structure well preserved in several species including *Camptosaurus*, *Iguanodon* and *Probactrosaurus*. Varying hypotheses have been offered in regard to the capacity of this unique arrangement which likely served a variety of functions including defence and breaking into seed and fruit (Norman 2004). It is not unreasonable to suggest that the digit was utilised during antagonistic encounters between mature breeding males, either as an instrument of bluff or use in physical combat. A common postcranial feature of many hadrosaurids was tall caudal neural spines, with those of *Hypacrosaurus altispinus* among the most dramatic (Morris 1978). Other hadrosaurids are known to have had a frill along the back which had a jagged appearance in *Edmontosaurus* and a more triangular look in *Kritosaurus* (Carpenter 1999). Such structures may have been used to exaggerate physical size during lateral displays between individuals or simply to differentiate species. In terms of quality and quantity of available material, the hadrosauridae are perhaps the best known dinosaur group and boast an impressive array of both solid and hollow supracranial crests (e.g. Alexander 1989; Godefroit et al. 2003; Horner et al. 2004). It is therefore appropriate to consider that these complex cranial structures served a pivotal role in terms of both physical and vocal courtship displays, while acting as signals to promote copulation specifically within a given species (Hopson 1975; Molnar 1977). As with other dinosaurs, these varied yet species-specific structures undoubtedly acted as mating signals and in that respect likely served as an important factor in speciation events (see Sampson 1997b, 1999).

The Pachycephalosauria are instantly recognisable due to the unique thickening of the skull roof, the purpose of which has drawn much controversy over the years and continues to do so. The earliest documented reference is that of Colbert (1955) who suggested in passing that the dome may have functioned as a battering ram, though no further explanation was offered. The first formal attempted explanation of this structure was proposed by Galton (1970, 1971), who suggested a scenario in which two competing males would run towards each other and slam their heads together in ritualised dominance displays similar to those of bighorn sheep. Alexander (1989, 1997) arrived at a similar conclusion, arguing that in a head-on collision the thickened skull roof would absorb most of the impact without inflicting serious injury. This idea was further explored in a functional study by Sues (1978) who found that the lateral walls of the pachycephalosaurid braincase were extensively ossified and that the frontal–parietal dome appeared oriented in a manner to transmit

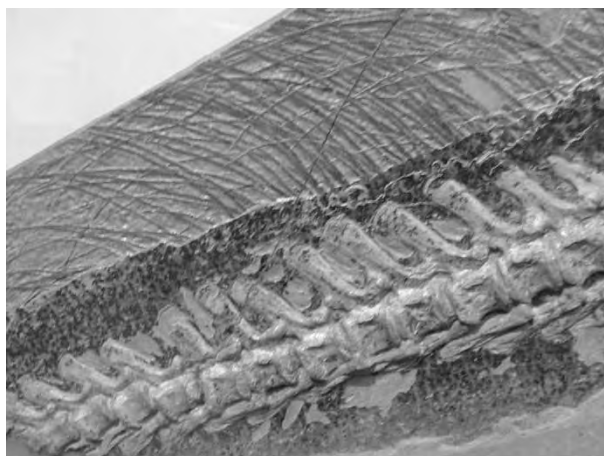


Figure 1. The integumentary structures of the ancestral primitive ceratopsid *Psittacosaurus*. Photograph courtesy Dr D. Martill.

stress. Sues concluded that these features were adaptations allowing for the transmission of stress during dome-to-dome impact. However, he recognised that both the lack of a self-correcting mechanism to avoid glancing blows and the rather limited surface area of the dome were serious confounding factors and thus suggested flank-butting as an alternative scenario.

This idea was further developed by Carpenter (1997) who suggested the flank-butting model inspired by the behaviour of African antelopes. In this model, the two opponents stood parallel, either facing each other or in the same direction, and delivered blows to the sides of each other's body. Carpenter further advocated two distinct types of flank-butting based upon the structure of the dome. Pachycephalosaurs such as *Stegoceras* and *Pachycephalosaurus* demonstrated type one combat in which the tall, round frontoparietal domes would maximise the force of impact of the head during flank-directed strikes without causing serious injury. Type two combat was proposed for *Stygomoloch*, a genus with squamosal horns along the posterior margins of the dome that could have been employed to inflict localised non-lethal discomfort (Carpenter 1997). Yet another conclusion was reached by Goodwin et al. (1998) while evaluating a well-preserved *Stygomoloch* skull, and braincase. The authors argued against head-to-head contact in this genus for a variety of reasons. First, the skull was too small and convex to have been used as a butting device. There was no correction mechanism to compensate for misalignment during a butting match, no shock absorbing sinuses in the skull, and in any putative head-to-head strike there would be serious damage inflicted to the nasals and lateral bones of the skull. Furthermore, upon examination the bone that composes the dome in *Stygomoloch* is highly vascularised and of a pattern that offers no substantial protection from directed impact force. It was concluded that the orientation of the squamosal horns and 'ornamental' nodes suggested a possible display function (Goodwin et al. 1998).

Goodwin and Horner (2004) examined the cranial histology of the frontoparietal dome with the intention of testing both the head-butting and an older heat dissipation theory and found no support for either. The highly vascularised, sponge-like bone cited by previous investigators as evidence for such behavioural and functional modes was found to be an ontogenetic growth stage of which there are three distinct histological zones. The authors conclude that the frontoparietal dome and associated cranial ornamentation served as a species recognition tool in the pachycephalosaurids. While sharing the caution raised in this study, Snively and Cox (2008) demonstrated confidently that the head-butting model could not be completely ruled out by employing a finite element analysis of adult *Pachycephalosaurus* and *Homalocephale* crania. They report that the domes could

withstand impact force at low collision speeds and that any force stress would tend to dissipate throughout the dorsal region of the skull before reaching the brain.

Despite these controversies and contradictory findings, the wide variation in dome shape and cranial ornamentation likely meant that aggressive behaviour among the pachycephalosaurids was equally varied. Intraspecific agonistic behaviour in mammals (see above; Geist 1966) demonstrates a gradual transition from flank-butting to head-to-head contact and finally displays function as ornamentation became more sophisticated. It is quite plausible that a similar scenario occurred among the pachycephalosaurids with the species having flattened domes more geared towards flank-directed attacks while those boasting a more rounded dome were better suited for head-to-head contact (see Maryanska et al. 2004). The highly vaulted cranial dome of *Stygomoloch* appears ill suited for either attack strategy or may have been purely for visual display. In that respect, it is conceivable that the dome may have undergone seasonal colour changes in either one or both genders and thus would have been a vital component in any putative courtship behaviour and species-specific recognition factors.

Sexual dimorphism has been suggested for certain members of both the stegosaurids and ankylosaurs in regard to skeletal attributes, but such putative differentiation remains unknown for either the dorsal plates or armour. A number of nodosaurids boast elongate spines on or near their shoulders and it has been suggested that these may have interlocked with those of an opponent during dominance bouts (Coombs 1990). Stegosaurids may have utilised their plates as sexual display structures and with the plates and spines arranged in a species-specific layout (e.g. de Buffrenil et al. 1986; Galton and Upchurch 2004). Other investigators have considered the possible role of armour and plates in intraspecific displays, with the structures acting as badge displays within a hierarchal social organisation (Davitashvili 1961 in Galton and Upchurch 2004). In a further nod to this theory, Spassov (1982) noted that the dorsal armour could have been a primary display organ during agonistic encounters in this group. It can be speculated that the complicated array of spikes, dorsal plating and body armour seen in the Thyreophora underwent seasonal colour shifts which could have been an integral part of any courtship, interspecific displays and species-specific mating.

Finally, the discovery of detailed fossilised skin impressions of diplodocid sauropods revealed unexpected structures in the form of a sagittal row of dermal spines over the tail which may or may not have continued along the body and neck. Further evaluation revealed that these narrow spines, which reached a height of 22 cm, are not simply extensions of the vertebrae and in terms of their overall appearance comparisons have been made to the dorsal spines of extant iguanas (Czerkas 1992, 1994).

More dramatic structures are known for the sauropod *Amargasaurus cazaui* in the form of a series of tall neural spines along the neck and back. At their tallest on the neck where they pair into two parallel rows, these spines continue down the back in a single row and undergo a noticeable decrease in height as they approach the sacrum (Salgado and Bonaparte 1991; Bailey 1997). It has been suggested that these unusual paired spines may have supported a set of twin 'sails' though this idea remains contentious. This ornamentation might have served a species-specific context and may have even undergone colour shifts during the mating season.

Discussions regarding visual display apparatus often make reference to the importance of colour as a factor in courtship displays or sexual dimorphism (e.g. Sampson et al. 1997). Competition for mates and the recognition of both species and gender have long been considered important functions of distinctive colour patterns in both birds and mammals (e.g. Geist 1977; Rohwer 1985; Hill 1990; Zuk et al. 1992). However, an important caution was proposed by Bennett et al. (1994) who questioned the reliability of employing colour as a measure of sexual selection. Birds and fish can perceive colour hues in a manner very different from humans who cannot, for example, distinguish ultraviolet light. The perception of colour can also be influenced by changes in background, ambient light, weather and time of day and is likely to be influenced by other trade-offs such as remaining conspicuous to a prospective mate and retaining a degree of crypsis to minimise detection by hostiles (e.g. Endler 1991). In that regard, the modern tendency to reconstruct dinosaurs with ostentatious colour schemes and garish patterns should be treated with a degree of scepticism.

2.4 Evidence for vocal apparatus

There can be little doubt that the crests, hornlets, spikes, armour and cranial ornamentation of dinosaurs could have served as species-specific recognition tools and display organs for courtship and intraspecific behaviours, much as observed in extant archosaurs. However, these particular structures are all geared towards visual communication. amongst the extant archosaurs, sound is a demonstrably important component of both courtship and intraspecific relations.

Sound production in crocodilians is similar to that of most vertebrates and is accomplished by the simple act of forcing air through the larynx in the throat (Fitch and Hauser 2002). Among extant archosaurs, the use of the larynx as a vocalising structure is unique to the crocodilians as the equivalent structure in birds serves strictly to prevent food from entering the lungs. With the sole exception of ratites, all avians employ a unique and highly specialised bony structure called a syrinx to produce sound. The syrinx is located at the lower end of the

trachea surrounded by an air sac where it works in synchrony with a series of elastic vibrating membranes to function as a resonating chamber. By controlling the tension applied to these membranes and the flow of air through the syrinx, birds can control volume, pitch and frequency of their calls (Fitch and Hauser 2002; Kroodsma 2004). The hearing sensitivity of both crocodilians and birds is approximately correlated with the relative length of the cochlear duct. Short lengths tend to signify a restriction to lower frequency sounds while in contrast elongated ducts demonstrate the ability to intercept higher frequencies. Such a scenario opens an interesting avenue for research regarding the possible responsiveness of certain dinosaurian taxa to audible signals (Sanders and Smith 2005).

Ever since Lambe (1914) found the lambeosaurine crest to be hollow and able to conduct air between the external nares and lungs, numerous explanations for this feature were proposed. Some early investigators considered these unique structures to be highly specialised adaptations for a primarily aquatic lifestyle, with the crests acting as either a snorkel (Romer 1933) or as a reservoir for stored air (Romer 1933; Colbert 1955) during instances of extended underwater feeding. Sternberg (1935) considered that the 'U' shaped layout of the narial loop would have been ideal to prevent water from entering the primary respiratory system. These ideas were disputed by Ostrom (1962) who established that the volume of air that could be held in the crests would have been meaningless compared to the animals' overall lung capacity. Furthermore, it has been well established that hadrosaurs were not exclusively aquatic (Horner et al. 2004). Other theories were that the hollow nature and placement of the crests served as a cooling mechanism for the brain (Wheeler 1978), whereas Ostrom (1962) thought that the extensive surface area provided by the hollow interior would have allowed for a dramatic increase in olfactory epithelium and thus enhanced olfactory perception.

Wiman (1931) was first to propose a workable socio-sexual explanation for the hollow crests of lambeosaurine hadrosaurs and considered the elongated narial cavities of *Parasaurolophus tubicens* to be functional resonating chambers through which males would call to attract females. The lambeosaurids have received particular attention in regard to possible vocal abilities due to the unique construction of their supracranial crests that are intimately interconnected with regions of the nasal cavity. CT scans of the enclosed narial chambers of *Hypacrosaurus* revealed the presence of a complicated network of bone which may have served to act in both olfaction and water retention during respiration (Horner 1995), although this conclusion was questioned in a re-evaluation by Ruben et al. (1996) based on an analysis of the cross-sectional area of the nasal passageways. Investigations by Weishampel (1997) and Diegert and Williamson (1998)

used acoustic models to demonstrate that the hollow crest was highly conductive to resonance, especially at lower frequencies. This confirmed previous conclusions that the primary function of the lambeosaurid crest was as a display-oriented species-specific visual and vocal communication device (Hopson 1975; Molnar 1977; Weishampel 1981; Alexander 1989; Evans et al. 2008), thus adding further credence to both social and potential courtship functions of hadrosaur cranial ornamentation.

Vocal abilities may have been shared by other hadrosaur groups. The skull of the non-crested hadrosaurine *Edmontosaurus* has circumnasal depressions excavated into the nasal bones which house a diverticulum which may have been covered by flexible integument. Upon closure of the external nares, the diverticulum may have been filled with redirected air and be inflated, causing the overlying integument to expand and swell in a dramatic visual display. If the stretched skin was to broadcast previously obscured bright colouration, such a scenario would have greatly enhanced the display value and it is quite probable that there was a vocal component to the behavioural cycle of this event (see Hopson 1972, 1975; Carpenter 1999; Horner et al. 2004). The ability to use inflatable nasal structures to amplify and transmit acoustic signals is a trait widely distributed among extant vertebrates and is well documented in anuran amphibians (Fitch and Hauser 2002) and mammals such as the elephant seal *Mirounga* spp. (Sanvito et al. 2007) and hooded seal *Cystophora cristata* (Berland 1965). Some birds can close their beaks and nostrils while exhaling into inflatable chambers located in the head and neck (e.g. Sutton 1977; Riede et al. 2004; Dantzker and Bradbury 2006; Bernard 2008).

The wide variety of theropod cranial ornamentation has already been discussed, though it is possible that some of these structures were involved in the transmission of sound. The hollow crest of *Monolophosaurus* has pneumatic connections to the nasal cavity suggesting that, in addition to a species-specific visual identity, the crest may have acted as a resonating chamber to amplify any sounds emitted. Some oviraptorids demonstrate a similar pneumatic crest whose internal structure appears to be associated with the nasal chambers (Currie 1997). However, it must be cautioned that basal avians and coelurosaurian theropods lack demonstrable evidence of a clavicular air sac homologous with that of extant avians, and in that respect it is highly unlikely that either groups possessed a syrinx [see (Senter 2009) for a detailed discussion].

Not all sounds produced by animals require a dedicated vocal apparatus and in that respect the production of non-vocal noise is a common phenomenon among both extant archosaur groups. Many crocodilian species utilise vigorous splashing behaviours to create a percussive display (Garriick et al. 1978; Kushlan and

Kushlan 1980; Tryon 1980; Kofron 1991; Thorbjarnarson and Hernandez 1993) along with jaw slaps in which the lower jaw is slapped against the surface of the water to create noise (Garriick and Lang 1977; Whitaker and Basu 1983; Whitaker and Whitaker 1984). Alligators engage in jaw claps, snapping both jaws together to emit a loud sound (Garriick and Lang 1977; Vliet 1989). Birds produce a considerable array of non-vocal sounds. During the breeding season, male ruffed grouse (*Bonasa umbellus*) attract the attention of females by rapidly beating their wings together to create low frequency sound waves. This drumming, colloquially known as spring thunder, is performed while the male perches on a fallen hollow log which serves as a resonating chamber (Allen 1987). The courtship behaviour of male American woodcocks (*Scolopax minor*) involves spiral flying in such a manner that air is moved rapidly through its firm outer primary feathers, causing them to vibrate rapidly and emit a high pitched twittering sound. A similar behaviour known as 'winnowing' is observed during courtship flights in the male common snipe (*Gallinago gallinago*) in which a series of shallow dives are performed during which the tail feathers are spread out so that the force of air passing over the stiff outer feathers causes them to vibrate and whistle. During the breeding season, male white-bearded Manakins (*Manacus manacus*) form leks and conduct a courtship display whereupon each male hops back and forth between twigs on saplings while emitting a 'snapping' sound produced by striking together the stiffened outer primary feathers. Other non-vocal sounds include the drumming of woodpecker species and the percussive jaw claps in birds as diverse as storks, tree swallows and roadrunners (Elphick et al. 2003; Podulka 2004). Considering the presence of non-vocal sound creation in both extant archosaur groups, it is reasonable to suggest that the phenomenon may have existed in the extinct archosaurian taxa – but is there any way to demonstrate this?

One of the more unusual hypotheses has been the putative role of the sauropod tail in possible acoustic displays. Alexander (1989) noted in passing that if the long, tapered tails of *Apatosaurus* and *Diplodocus* were flicked in a manner that caused the tip to move at supersonic speed, they could have been employed to make a considerable noise. This idea was explored in greater detail by Myhrvold and Currie (1997) who used computer models of *Apatosaurus louisae* tails to demonstrate that such physical movement and velocity attainment were not unreasonable. Specific lengthening of the caudal vertebral centra was considered an adaptation to counter the stresses generated, as was fusion of the caudal vertebra. The authors suggested that the noise produced would have been used for communication, defence and courtship with the latter suggesting the possibility of sexual dimorphism. However, this was questioned by Carpenter (1999) who noted that the distal end of the tail likely would have

required a flap of living skin acting as a 'popper' to effectively produce the 'cracking' sound. In such a scenario, the skin of the popper would rapidly become frayed, then scab over, and as scab tissue is very hard, any further use in noise production would be negated. It is interesting to note that the phenomenon of caudal vertebral fusion, which has been interpreted as a sexually dimorphic feature, has been attributed to not just one but both genders. Myhrvold and Currie (1997) considered it a male trait and its presence as evidence for courtship, intraspecific signalling and sexual display, whereas Rothschild and Tanke (1991) and Rothschild (1994, 1997) suggested a female attribute which would have allowed the tail to be held in such a manner as to effectively expose the cloaca and enable penetration when mating as discussed above.

2.5 Evidence for gregarious behaviour and social organisation

The nature of fossilisation makes any reference to or discussion of putative social organisations and gregarious behaviour difficult, though some essential ideas can be gleaned from the analysis of footprint trackways and monospecific mass death assemblages, both of which are useful indicators as to whether or not dinosaurs moved about in groups. Gregarious behaviour is a common phenomenon among extant vertebrates (e.g. Alcock 1989; Grier and Burk 1992), although when evaluating trace fossils one must be cautious to distinguish between taxa that might have legitimately lived in social groupings and those that simply lived in close proximity due to either a common habitat choice or simple chance. Dinosaur tracks offer a wealth of data from species range to biostratigraphic zonation in addition to yielding evidence for gregarious behaviour, which is usually inferred from a number of tracks that tend to be oriented in the same direction. Trackways can also provide valuable clues as to putative herd size, juvenile–adult ratios and the relative positioning of different size/age classes when travelling (see Lockley 1986a, 1994, 1997).

Bird (1939, 1941, 1944) was among the first to undertake a detailed evaluation of dinosaur trackways and described 23 individual sauropod trackways at the Davenport Ranch in central Texas. The extent of overlap of the footprints suggested that the majority of the dinosaurs were moving in more or less a straight line with larger individuals initiating the lead. Bakker (1968, 1986, 1997) interpreted the scenario as evidence of an advanced social organisation that included parental care with older animals apparently encircling and protecting the smaller and presumably more vulnerable young. This viewpoint was revised by other investigators in that the animals were simply travelling in a 'staggered or spearhead formation' with the larger and presumably faster members

progressing ahead of the smaller (Lockley et al. 1986). There are numerous similar tracksites in North America including the Purgatoire River site in southeastern Colorado, where more than 100 trackways are preserved, apparently left by the sauropod herds that once travelled across the mudflats along the perimeter of inland seaways (Lockley 1986b, 1991; Lockley et al. 1986), and further tracks can be found at the Hidden Canyon locale in Utah (Barnes and Lockley 1994).

Evidence of sauropod herding behaviour is found throughout the globe (e.g. Farlow 1987a; Lockley et al. 1994a) with well-preserved trackways in Portugal (Lockley et al. 1994b; Santos et al. 1994), Spain (Schulp and Brokx 1999), Patagonia (Coria 1994), the Banos del Flaco Formation in Chile (Moreno and Benton 2005), Bolivia (Lockley et al. 2002a), **Switzerland (Marty et al. 2003)**, China (Chen and Huang 1993; Lockley et al. 2002b) and the Arabian Peninsula in the Middle East (Schulp et al. 2008). **Multi-species herds of sauropods have been reported from Oxfordshire in the United Kingdom (Day et al. 2004)** which were likely the result of several species following a similar route. Sauropod track assemblages tend to occur where there were once coastal lagoons, saltwater lakes and other marginal marine environments (e.g. Leonardi 1989; Lockley 1991). **As these habitats are among those in which footprints are most likely to survive the process of fossilisation, it has been suggested that this association may represent either preservational bias or a behavioural artefact of animals following the shoreline during migration events** (see Farlow 1992).

Putative herding activity is by no means limited to sauropods and has been described for other dinosaur groups. At locales in both Price, Utah, and the Mesaverde Formation in Grande Mesa, Colorado, there is an abundance of hadrosaur footprints that have been interpreted as evidence for herding behaviour in these animals (Carpenter 1992). Further evaluations of the trackways at Grande Mesa suggest that herds were composed of both mixed species herds and differing age classes, the latter of which has led to suggestions of possible post-hatching parental care (Lockley et al. 1983). Ornithopod herds of the ichnogenus *Caririchnium* are found in such numbers at the Dakota Group in Colorado and New Mexico that the megatracksite is colloquially referred to as the 'Dinosaur Freeway' (Lockley and Hunt 1995a). Discoveries at the Peace River locale in British Columbia have yielded extensive parallel trackways of both adults and juveniles of the bipedal ornithopod ichnogenus *Amblydactylus* (Currie 1983, 1995). Further, hadrosaur footprints have been found at the Cerro Del Pueblo Formation of Coahuila, Mexico (Rodriguez-de la Rosa 2007). Herding evidence for the Thyreophora and Ceratopsia are rare (e.g. Hunt and Lucas 2006) with the only multiple trackways of ankylosaurs being those for the ichnogenus *Tetrapodosaurus* from the Gates Formation Near Grande Cache, Alberta (Carpenter 1984; McCrea and

Currie 1998) and a group of small ankylosaurids from the Dakota Group in southeast Colorado (Lockley et al. 2006). Lockley and Hunt (1995b) found probable ceratopsid tracks at the Laramie Formation of Colorado.

Individual footprint tracks of theropods are not uncommon (e.g. Lockley and Hunt 1995a, 1995b; McCrea and Currie 1998; Rodriguez-de la Rosa 2007), although trackway evidence that suggests widespread gregarious behaviour among this group appears to be rare. Indeed, Lockley (1991) noted that compared to sauropod and hadrosaur trackways, those of theropods tended to demonstrate considerably less spacing between tracks and were more random in orientation. Some of the evidence for gregarious behaviour in theropods have been based upon two or more parallel tracks oriented in the same direction as those of their putative prey (e.g. Rogers 2002) and in that respect Lockley (1991) suggested two such scenarios. A set of trackways from the Dinosaur Valley State Park in Texas appeared to depict three individual theropods following and presumably stalking a small herd of sauropods, and another trackway from Bolivia was interpreted as several theropods following a herd of sauropods. It should be noted that Lockley's first example was evaluated by Farlow (1987b) as only a single predator shadowing the herd. Despite the rarity of theropod trackways, there are a few particular examples that deserve mention and critique.

The earliest documentation was made at the Mount Tom site in Massachusetts, USA, by Ostrom (1972), who described nearly 20 parallel trackways which were considered to be left by a large group of small theropods travelling in the same direction at the same time. This particular interpretation was challenged by Coombs (1990), who demonstrated that the trackmakers were likely individuals travelling independently along the edge of an ancient shoreline. Clark et al. (2005) described trackways at the Kilmaluag Formation on the Isle of Skye, Scotland, which they interpreted as evidence of a theropod family group of adults and juveniles. However, the very small surface area cited in the study (about 1.5 m²) makes such a conclusion tenuous and all that can be reliably inferred is that a group of differing size classes of the same ichnospecies, travelling in the same direction, crossed the area over a short time period (after Roach and Brinkman 2007). One of the more curious claims regarding alleged sociality in theropods was offered by Lingham-Soliar et al. (2003) who reported multiple trackways at the Dande Sandstone Formation in Zimbabwe as representing a group of theropods travelling in a distinct group. However, the fossil evidence clearly shows trackways spread across several orientations and it is not known why the authors decided to interpret this as evidence of gregariousness when the tracks are so highly random. Matsukawa et al. (1997) described a detailed trackway left by 33 members of the ichnogenus *Toyamasauripus masuiae* from the

early Cretaceous beds of Toyama prefecture in central Japan and from Shandong, China, Li et al. (2007) reported both closely spaced and multiple parallel trackways considered as evidence for group travel in deinonycho-saurs, though no inference to pack hunting was made. The Winton Formation in Queensland, Australia, is famed for the Lark Quarry site which boasts trackways preserved in an ancient mudflat of over 130 small theropod and ornithopod dinosaurs, which apparently went into a stampede triggered by the approach of an individual large theropod (Thulborn and Wade 1979, 1984). It is unknown as to whether or not the trackmakers were adult animals or juveniles living in a temporary group, though if the former should be the case then the Lark Quarry site would represent substantive evidence that at least one particular theropod species demonstrated gregarious traits.

Monospecific skeletal associations are another possible indicator of gregarious behaviour or herding in dinosaurs. The earliest documentation of a mass accumulation was described by von Huene (1928) who interpreted the bonebeds of the prosauropod *Plateosaurus* found at Trossingen, Germany, as evidence of seasonal migration with weaker animals perishing along the way. The El Tranquilo Formation in South America has yielded a similar mass accumulation of *Plateosaurus*, though it remains unknown if this assemblage was due to either accretional or catastrophic causes (see Coria 1994). This is by no means a unique occurrence as records for assemblages of sauropod skeletons are well documented (e.g. Dodson et al. 1980b; Jain 1980; Coria 1994; Heinrich 1999), adding further support for herding and gregarious behaviour. Perhaps the most famous mass assemblage was that of 24 individual and several more partly preserved specimens of *Iguanodon bernissartensis* found in a coal mine near Bernissart, Belgium. The spectacular preservation of both adults and juveniles is believed to have been due to a sudden natural disaster such as a mudslide or a flash flood (Norman 1980, 1987). Further hadrosaur bonebeds are well documented at formations in Price, Utah, and Grande Mesa, Colorado (Carpenter 1992), and those in North America appear to be monospecific (Hooker 1987; Varricchio and Horner 1993). The Cedar Mountain Formation in eastern Utah has yielded a monospecific bonebed of at least 12 specimens of the ankylosaur *Gastonia bergei* (McWhinney et al. 2004). The only record of a stegosaur assemblage is an unpublished report from the Morrison Formation of Montana, where preliminary excavations have uncovered what appear to be two adult and two subadult specimens of *Stegosaurus armatus*, though a more thorough investigation is currently ongoing (S. Maidment, Judith River Dinosaur Institute, personal communication).

Dodson (1971) was among the first to note the presence of multiple ceratopsian skeleton quarries in the Judith River Formation, and the Province of Alberta

in Canada has yielded several ceratopsid assemblages. The Dinosaur Provincial Park boasts accumulations of *Centrosaurus*, *Styracosaurus*, *Monoclonius* and *Chasmosaurus* (Sternberg 1970; Currie and Dodson 1984; Eberth and Getty 2005). Several impressive bonebeds of *Centrosaurus apertus* have long served as a case study for evidence of herding behaviour in ceratopsids. The assemblage is considered to have been the result of a natural disaster in which possibly thousands of the animals were drowned and gradually transported by current flow (Currie 1989; Dodson et al. 1994; Ryan et al. 2001). Monospecific bonebeds tend to be located in the lower portion of the Judith River Formation which has been considered evidence that the animals lived in large herds some distance from the shoreline (Eberth 1996). However, further evaluation of both stratigraphic and paleogeographical patterns indicates that ceratopsids were found in far greater abundance in coastal areas than inland regions. The apparent contradiction in distribution patterns suggested by the two datasets was reconciled by proposing a seasonal difference in distribution, with the animals nesting in one area, then migrating to avoid environmental stress (after Brinkman et al. 1998). A mass mortality of *Pachyrhinosaurus* was reported by Tanke (2005) from Pipestone Creek bonebeds in northwestern Alberta, where the presence of four distinct size classes provides further evidence that these gregarious animals travelled in large herds. It is suspected that drought conditions were a major killing agent in these events (Dodson et al. 2004) and in similar mass mortalities in Montana (Rogers 1990). Until recently all *Triceratops* specimens represented solitary individuals, an observation that suggested this genus as unique in contrast to other apparently more social ceratopsids. A recent discovery from southeastern Montana of three juvenile *Triceratops* suggests that the young formed exclusive groups, though it is not known if this was a temporary or extended phenomenon (Mathews et al. 2009).

Theropod bonebeds are well documented. Eberth et al. (2000) reported a monotaxic group of at least six carcharodontosaurs from the Rio Limay Formation in Argentina which appeared to be the result of a mass mortality, though the cause of death was not apparent. The Ghost Ranch in northern New Mexico is known for its remarkable yield of at least 1000 complete and partial specimens of *C. bauri* (Colbert 1990). Believed to have been caused by a drought event (Schwartz and Gillette 1994), this discovery remains perhaps the most impressive of all mass death assemblages in terms of the sheer quantity of skeletal material. Partial remnants of more than 30 *Syntarsus rhodesiensis* were found in Zimbabwe, Africa, which was believed to have been the result of a catastrophic event of unknown origin, although lithology of the bonebed indicates a highly arid environment at the time of death (Raath 1990).

An association of at least nine *Albertosaurus sarcophagus* has been reported from the Horseshoe Canyon Formation in Alberta. Based upon the skeletal dislocation, taphonomic condition, minimal presence of herbivore remains and the lack of tooth marks on the bones, Currie (1998) concluded that the assemblage was not the result of a predator trap but rather evidence of a group of *Albertosaurus* living together. Currie further proposed that the assemblage demonstrated evidence of pack hunting in tyrannosaurids with division of labour, envisioning the smaller and apparently faster juveniles targeting fast moving prey such as ornithomimids which could easily escape larger members of the pack. Roach and Brinkman (2007) countered with a reinterpretation that the remains, which were composed primarily of inedible tail sections and feet, were more likely the result of intraspecific predation, itself by no means unknown in theropods (e.g. Rogers et al. 2007).

Another tyrannosaurid bonebed was discovered in the Two Medicine Formation of Montana and described by Currie et al. (2005a). Three or more specimens of the genus *Daspletosaurus* appeared to be intermingled with the remains of approximately five hadrosaurs. The apparent lack of sorting and the presence of fully articulated portions of skeletons led the authors to conclude that a social group of *Daspletosaurus* had been feeding upon the herbivores when the entire assemblage was buried simultaneously. It was further claimed that a social grouping of sorts would have been necessary for the predators to counter the defences of their prey. A re-evaluation of the evidence by Roach and Brinkman (2007) demonstrated that the hadrosaur carcasses had more likely been transported to their final position by floodwaters and then extensively preyed or scavenged upon by a large number of individual tyrannosaurids. The associated remains of *Daspletosaurus*, which like the above scenario were dominated by inedible foot bones, were most likely those killed by conspecifics while scavenging the remains of the hadrosaurs. Both the Horseshoe Canyon and Two Medicine tyrannosaurid assemblages appeared to have been the result of seasonal stresses or droughts (e.g. Gates 2005) during which prey availability would have been limited and thus the potential for intraspecific competition over resources would have been high, a situation that has strong parallels with extant crocodilian populations (e.g. Pooley and Ross 1989; Rootes and Chabreck 1993).

The Cleveland-Lloyd Quarry has yielded numerous specimens of *A. fragilis*, though this assemblage has been interpreted as either a predator trap (Madsen 1976; Miller et al. 1996; Richmond and Morris 1996) or the aftermath of a drought event (Gates 2005) and is not considered to represent evidence of any social formation (see also Roach and Brinkman 2007). A *T. rex* specimen from the Hell Creek site in eastern Montana colloquially known as 'Sue' was reported to have been found in a quarry that contained

the remnants of three alleged conspecifics (another adult, a juvenile and an infant) which was interpreted as part of a functioning social group (Larson 1995, 1997; Currie 1998; Erickson 1999), though it is not clear if these were animals that had been killed and scavenged by conspecifics, which based upon aforementioned evidence appears to have been a common phenomenon among theropods.

There are instances of monospecific bonebed records that have been reported for the Ornithomimosauria. These assemblages include *Archaeornithomimus* at Iren Dabasu (Currie and Eberth 1993) and at least 20 specimens of *Sinornithomimus dongi* from the Ulansuhai Formation of the Nei Mongol region of China (Varricchio et al. 2008b). The unusually large numbers of mixed-age juveniles in the latter aggregation led Kobayashi and Lu (2003) to suggest that gregarious behaviour might have served as an anti-predator tactic in this particular species. However, as most ornithomimid remains tend to be found apart from each other, it is not known whether these aggregations of animals represented perennial or seasonal events (Makovicky et al. 2004).

Evidence from trackways and mass assemblages clearly indicate that at least some dinosaurs were gregarious, which would indicate that some sort of social organisation was present. The mating systems of extant archosaurs tend to be rather diverse. Crocodilians tend to be polygynous with both sexes staking out and defending territories to secure breeding access and preferential nesting sites, respectively. In some populations of Nile crocodiles (*Crocodylus niloticus*), apparent instances of seasonal monogamy have been documented (e.g. Pooley and Gans 1976). The mating system of the Orinoco crocodile (*Crocodylus intermedius*) is known to incorporate both monogamy and polygyny, though in both of these cases the mating system appears to be strongly influenced by overall population density. In high-density populations, a dominance hierarchy prevails in which a single dominant male secures the majority of matings while at lower densities monogamy may occur (Kofron 1991).

In contrast, there are a variety of partnerships and mating systems present in extant birds which are summarised thus:

- (1) *Monogamy*. Although about 90% of avian species appear to demonstrate exclusively monogamous pairing (Lack 1968), the relationships are frequently much more complicated than initial appearances (Ligon 1999). It has been shown in many species that successfully raising offspring together neither requires nor implies fidelity between the parents, with many apparently monogamous species engaging in extra-pair copulations with other partners during the breeding season (e.g. Bjorklund and Westman 1983; Smith 1988; Birkhead and Møller 1995; Møller and Tegelstroem 1997; Hasselquist and

Sherman 2001). It has been suggested that extra-pair copulations act to increase the genetic diversity of offspring or to allow a female to produce young sired by a higher quality male than her previous choice (Elphick et al. 2003). In regard to the latter point, Kempenaers et al. (1992) demonstrated that male blue tits (*Cyanistes caeruleus*) with superior ornamentation and territories were not only solicited for more extra-pair copulations, but also ended up with far fewer non-related chicks in their own nests. It is now widely accepted that true monogamy, in which only a single male and female are the genetic parents of offspring, is the exception rather than the rule in the overwhelming majority of extant avians (see Elphick et al. 2003).

- (2) *Polygyny*. While the vast majority of animal species practise polygyny (Alcock 1989), it is estimated that only about 2% of avian species employ this particular mating system. A polygynous relationship is one in which a successful dominant male secures a number of mates, though in comparison females have only one mate, at least during a particular breeding season or cycle. In birds, polygyny is often associated with habitats where a female can locate and exploit enough food without assistance and hatchlings tend to demonstrate a high degree of independence, both vital traits as the males often provide no parental care (Elphick et al. 2003). There are three distinct variations of polygyny.

Resource defence polygyny occurs when resources essential to females tend to be clumped and as such can be defended by males, a classic example of which is the red-winged blackbird *Agelaius phoeniceus* (Beletsky 1996; Pribil and Picman 1996). Polygyny increases male reproductive success by means of allowing him to monopolise matings, though for females the benefits are less clear. One model predicts that should variation between an occupied territory and an unoccupied territory exceed a certain theoretical level known as 'the polygyny threshold', then in terms of a female's fitness it is far more advantageous to opt for polygyny in a superior territory than monogamy in a lower quality territory (Verner and Wilson 1966; Orians 1969). It is thought that the benefit of a territory with more exploitable resources can overcome negating factors such as a lack of parental assistance or help from a polygynous mate [see Oring (1982) and Searchy et al. (1999) for more detailed discussions].

Female defence polygyny occurs when females tend to aggregate in a specific area and if they can be defended by a male against competitors he can obtain a substantive number of matings (Grier and Burk 1992). This behaviour is well documented in mammals (e.g. Cox 1981; Clutton-Brock et al. 1982;

Ortega and Arita 2000), but tends to be a rather unusual occurrence among birds, having been noted primarily in the neotropical blackbird Montezuma Oropendola, *Psarocolius montezuma* (Webster 1997).

Male dominance polygyny differs considerably from the previous variants in that there are neither aggregations of females nor resources over which to gain exclusive control. In this system, the females choose males with polygyny being the result of consensus among the females in regard to which males are the most desirable (Grier and Burk 1992). Commonly, this is termed a lek, defined as a group of males who aggregate to perform courtship displays while defending a small patch of territory. Lekking is known in 14 bird families worldwide and is especially well documented among grouse and prairie chickens (Elphick et al. 2003). Lek mating systems tend to be defined by (1) absolutely no male parental care; (2) males being distributed in territories that are spatially clustered; (3) territories that contain no useful resources that might act to influence female choice and (4) females are able to choose freely from potential mates within the cluster of male territories (Bradbury 1985; Grier and Burk 1992). Males that lek can be sexually dimorphic, sporting bright, exaggerated plumage and inflatable throat sacs, whereas females tend to be physically smaller and either more drab or cryptically coloured. Males display to both competitors and female visitors with the latter choosing the most dominant vigorous males who are able to attract a higher number of potential mates (Wiley 1978; Grier and Burk 1992). There are numerous competing theories in regard to where and why lekking occurs (e.g. see Bradbury and Gibson 1983; Beehler and Foster 1988), though it appears that females may prefer large clumps of males because it facilitates mate choice (Grier and Burk 1992). However, Elphick et al. (2003) noted that lekking tends to be persistent in regions where males control neither food resources nor females and thus have simply their phenotypic qualities to advertise to potential partners. For males who manage to reach the upper levels of the dominance hierarchy, the pay-off in reproductive potential is high, whereas females are able to more easily select from males than they could in a more isolated environment.

- (3) *Polyandry*. Of all mating systems, polyandry is the rarest and has only been documented in about 1% of birds (Elphick et al. 2003). Polyandry is most commonly used in reference to a single female forming pair bonds with multiple males, though the phenomenon actually has two distinct variations: classic polyandry in which males establish individual nesting sites whereupon a single female mates with each one, and cooperative polyandry where a group

of males will share breeding access with a female (see Oring 1986). The former is well known in the Rallidae, the northern jacana (*Jacana spinosa*) and the spotted sandpiper (*Actitis macularia*) in which polyandry has been extensively studied (Elphick et al. 2003). In the latter species, a female copulates with and subsequently deposits eggs in the nests of several different males who each assume sole responsibility for the incubation and rearing of their clutch. The traditional sex roles are thus reversed with the females actively defending territory, courting individual males and competing with other female conspecifics for access to mates (Hays 1972), although it should be noted that the degree of polyandry expressed tends to be strongly correlated with the overall sex ratio (Oring et al. 1983). Perhaps the best example of cooperative polyandry is to be found in the Tasmanian Native Hen (*Tribonyx mortierii*) in which a pair of brothers breed a single female with all genders assuming a permanent breeding group sharing responsibility for nesting, incubation and care of the young. It has been suggested that perhaps the unusually high ratio of male to female hatchlings may provide an explanation for this unusual mating system (Smith and Ridpath 1972), though Oring (1986) suggested other possible causes, such as harsh ecological conditions requiring a larger number of individuals to successfully raise young.

- (4) *Polygynandry*. Only a very few avian species demonstrate polygynandry, which can be defined as several males and several females in a breeding group in which there may or may not be long-term bonds between the members (Grier and Burk 1992). The best known example of this unique arrangement is the Dunnock (*Prunella modularis*) where both males and females establish overlapping territories which are defended against members of the same sex. Male territories are as large as possible, whereas females are based upon maximising access to feeding sites. Dependent upon these overlapping territories, multiple mating systems are present and can include monogamy, polygyny and polyandry, with polygynandry resulting when the territories of several males overlap those of several females. The situation can become complicated, though the ability of males to monopolise females in either monogamous or polygynous relationships ultimately depends upon distribution and abundance of food supply (see Davies and Lundberg 1984; Davies 1985; Grier and Burk 1992). Polygynandry in Smith's Longspur (*Calcarius pictus*) and the Acorn Woodpecker (*Melanerpes formicivorus*) has also been documented (Elphick et al. 2003).

There is an interesting dichotomy in the nearly exclusive presence of polygyny in crocodilians versus the comparatively much wider range of social mating systems observed in birds. The proximate and ultimate causes for this difference are unclear but are likely to involve variations in reproductive biology, nest attendance, habitat, nutritional requirements of neonates and incubation methodology between the two groups. As an example, crocodilians employ heat derived from rotting vegetation to incubate their eggs, whereas birds (with the sole exception of the megapodes), rely upon almost constant direct physical contact with their eggs throughout the incubation period to maintain a particular thermal regime. This means that a parent must attend and incubate the eggs until the time of hatching, a prerequisite that requires more than one individual and as a result may set the stage for a greater variety of social organisations and relationships.

But what does any of this tell us of dinosaurs? It is extremely difficult to discuss the possible mating systems of the extinct Archosauria beyond the realms of speculation as there is such precious little substantial evidence to build upon. The idea of social behaviour in reptilian grade vertebrates, including the Dinosauria, has long been subject to derision (e.g. Colbert 1961), much of which was based upon a combination of very poor field ethology and flawed early laboratory experiments that ignored the subject animals' unique thermal and micro-habitat requirements. Brattstrom (1974) demonstrated conclusively that when captive reptiles were provided with the required ambient temperature and moisture regimes, they could easily perform a variety of complex learning behaviours in subsequent tests.

Recent advances are fuelling a little known, yet growing renaissance in terms of how reptile behaviour is viewed. It was previously thought that only mammals and birds were capable of play behaviour (see discussions by Burghardt 1982, 1988), though play has now been either observed or recorded in lizards (e.g. Hatfield 1996; Burghardt 2002; Burghardt et al. 2002; see also Hill 1946), chelonians (e.g. Burghardt et al. 1996; Burghardt 1998; Kramer and Burghardt 1998) and crocodilians (e.g. Glickman and Sroges 1966; Lazell and Spitzer 1977; Divyabhanusinh 1986). Perhaps the most revealing studies have been of the social abilities of *Varanus komodoensis* and *Iguana iguana*. Burghardt et al. (2002) reported a variety of sophisticated behavioural routines in Komodo dragons, including less stereotypic and more graded levels of communication, the importance of spatial memory, rapid discrimination learning and the cognitive complexity to track both the location and previous productivity levels of food resource patches. In captivity, true play behaviour was conclusively documented in terms of both object-oriented play activity and interactions with zookeepers (e.g. tug-of-war games). Neonate reptiles often demonstrate a diverse

array of social behaviour which appears to have been long overlooked (e.g. Burghardt 1977; Burghardt et al. 1977). A remarkable example of this diversity is seen in neonate green iguanas which have been found to develop complicated anti-predator strategies, including group-based tactics in which males voluntarily sacrifice themselves to protect their female siblings (Rivas and Levin 2004).

Hopson (1977) further relied upon the behaviour of extant reptiles to argue for similar patterns in dinosaurs, including the evaluation of dinosaur brain endocasts from which an approximate brain to body mass ratio could be calculated. Known as an Encephalisation Quotient (E.Q.) (Jerison 1973), this formula suggested that theropod dinosaurs in particular, may have been able to express more advanced behaviours. However, the overall reliability of the E.Q. was questioned by Holloway (1979) who argued that growth in the mammalian neocortex is responsible for the evolution of advanced behavioural plasticity and that, furthermore, brain weight serves as an unreliable indicator of the internal structural complexity of the brain. This was further stressed by Deacon (1997) who coined the term 'Chihuahua Fallacy' in reference to the difficulty of extricating selection on brain size as opposed to body size. More recent experimental analysis by Burish et al. (2004) recognised the problem of relying upon absolute brain size and suggested a set of volume fraction calculations known as a 'cerebrotyping'. There is a strong correlation between the relative size of the telencephalon (the cerebral hemispheres) and overall degree and complexity of social interaction. Values for *Allosaurus*, *Tyrannosaurus* and *Carchardontosaurus* were found to be either at or below the range described for extant reptiles (Larsson et al. 2000). Interpolating the correlation to include *Archaeopteryx* indicated the social complexity of a chicken, which led Burish et al. (2004) to suggest a lifestyle that was likely to be either solitary or in very small groups.

The only substantive evidence that can be gleaned from the fossil record is that herbivorous dinosaurs almost certainly lived and travelled in herds or units containing individuals of varying age and size classes, a situation that implies some type of social organisation within the group. While there are large aggregates of small theropods such as *C. bauri*, no related trackway evidence appears to exist, which does not fit in with the idea that the animals remained permanently in large groups. It is possible that the aforementioned bonebeds simply represented an artefact of either common habitat choice or a particular stage in their reproductive cycle (Farlow 1987a). By stark contrast, the extensive and rich trackway evidence, associated mass accumulations, representation of different size classes in both the former and latter and the types of cranial ornaments documented in herbivores all conspire to present a very different picture. Extant vertebrate

herbivores tend to form herds as an antipredator strategy, which yields several highly specific benefits:

- (1) *Visual detection.* A large number of animals are more likely to visually detect danger at a distance, which means that a predator has less chance to attempt or initiate a successful attack. Combined with the effective use of warnings or alarm signals, if one member detects a threat then conspecifics are thus informed and can react accordingly.
- (2) *Geometry of the selfish herd.* Hamilton's (1971) hypothesis suggests that aggregations form for the purpose of putting others between oneself and danger; it is safer to be in a centralised position within the herd than on the periphery where a predator is more likely to pick off stragglers.
- (3) *Physical defence.* A herd allows for the possibility of an uncoordinated yet efficient collective defence against hostile incursion.
- (4) *Dilution effect.* This hypothesis proposes that the risk of predation to an individual may decrease as the number of individuals in a group increases and
- (5) *Cryptic avoidance.* A large herd undertaking chaotic multi-vectored evasive movements can act to confuse a predator by making it difficult for the hostile to successfully target a specific individual (after Hamilton 1971; Alcock 1989; Grier and Burk 1992).

Herds frequently demonstrate a dominance hierarchy in which higher ranked individuals locate themselves in preferred positions near the centre of the herd, where risks from predation are minimal (see Christman and Lewis 2005). Again it is interesting to note that in comparison to herbivorous dinosaurs, evidence of herding or group behaviour in the predatory theropods tends to be minimal. The few records of parallel theropod trackways would appear to represent temporary movement of individuals, perhaps drawn by flooding events and other seasonal phenomena that likely resulted in large deposits of carcasses (Dodson et al. 1980b). Such a resource would represent an opportunistic attraction to a variety of scavenging predators as can be deduced from shed teeth records (e.g. Bakker and Bir 2004), and it has been suggested that this may provide the explanation for a good number of theropod trackways (Roach and Brinkman 2007).

Dromaeosaurids have been portrayed as the dinosaurian equivalent of wolves, living in sophisticated social structures and hunting larger prey in packs. This has been the case since the remains of several specimens of *Deinonychus antirrhopus* were found in close association with the ornithomimid *T. tilletti*, a situation interpreted as evidence that the animals hunted in coordinated packs similar to wolves or African hunting dogs (e.g. Ostrom 1969; Bakker 1986; Maxwell and Ostrom 1995). Numerous problems exist with the pack hunting theory, which have been discussed in detail by Roach and Brinkman (2007). No

extant archosaur engages in the group hunting of prey too large to be taken by a single predator, though there are some examples of cooperative hunting. Certain crocodilian species engage in commensal feeding strategies to increase efficiency of intercepting fish and rendering carcasses. Spectacled caiman (*Caiman crocodilus*) are known to employ group tactics when fishing by positioning their bodies across narrow riverways and channels in a staggered step formation like a weir (Schaller and Crawshaw 1982; Thorbjarnarson 1993). A similar tactic has been reported and apparently overlooked in alligators (*Alligator mississippiensis*) which cooperatively feed near the water pouring from culverts (King et al. 1998). The phenomenon has been well documented in Nile crocodiles (*Crocodylus niloticus*) which not only employ this group fishing technique but will also work together to dismember floating carcasses, patiently taking turns as one animal tears off chunks of meat while the others hold the prey securely in place (Pooley and Gans 1976; Pooley 1982, 1989). Among birds, cooperative hunting is limited to the capture of comparatively small prey by a single member within a very small attacking group. The only exceptions are the 'mobbing' attacks of the Black Vulture (*Coragyps atratus*) and instances of two or more Golden Eagles (*Aquila chrysaetos*) targeting ungulates by repeatedly raking the prey's back with their talons. However, upon careful examination, both of these examples appear to be recently derived and highly specialised behaviours brought about by extreme environmental or seasonal conditions (see Roach and Brinkman 2007). It is clear that the use of pack-hunting mammals as models for dinosaur social organisation makes little evolutionary sense, as the nature of cooperative hunting in extant archosaurs is significantly different from that in mammals. It has been demonstrated that other diapsid models, in particular the hunting strategies and feeding site hierarchy patterns of varanids such as *V. komodoensis* (e.g. Auffenberg 1972), represent a more parsimonious template for theropods, especially in consideration of current fossil evidence [see Roach and Brinkman (2007) and references within for detailed discussions].

2.6 Evidence for mating, nesting and parental care

Minimal data concerning genital structures or reproductive system schematics are available for dinosaurs, a situation not surprising considering the rarity of fossil soft tissues and the level of conjecture that tends to dominate any such discussion. Before evaluating the presence of any putative sexual structures in dinosaurs, it is necessary to review the basic structural layout of the reproductive systems present in extant archosaurs and other reptiles. It is first necessary to briefly mention a particular aspect regarding the appropriate use of terminology. The males of all mammals, reptiles (except Sphenodontidae) and

paleognathae employ an intromittent organ for copulation for which the term 'penis' is often used colloquially. However, the mammalian penis is an organ structurally unique to its class, having an internal tube for seminal transport and a dual function for both urination and ejaculation (e.g. Campbell 1990). As such the term 'penis' should not be used in reference to the intromittent organ of non-mammalian vertebrates and instead the term 'phallus' is employed.

2.6.1 Description of the cloaca and reproductive structures

The cloaca serves as the common terminal chamber for the digestive, urinary and reproductive tracts of most extant vertebrates and exits to the outside via a cloacal opening or vent. This is in contrast to the Actinopterygii and placental mammals in which the cloaca is absent and instead the intestine opens to the outside via the anus, itself a separate opening from the urogenital system (Campbell 1990). The cloaca is divided into three distinct compartments with each controlled by muscular sphincters that act to regulate the entry and release of products received from the intestine, kidneys and gonads. The coprodeum is the most proximal compartment into which the intestine empties, followed by the urodeum where products from both the urinary and genital ducts are received. The most distal compartment is the proctodeum, which functions in copulation and in many amniotes develops and houses a phallic structure. Each of the three compartments is separated from the others by either muscular sphincters or specialised folds in the mucosal wall of the cloaca. The ectocoprodeal fold is situated between the intestine and coprodeum, the coprourodeal fold between coprodeum and urodeum and the uroprotodal fold between urodeum and proctodeum. It should be noted that it is not always easy to delineate specific boundaries between components of the cloaca, especially in fish (Kardong 1995).

2.6.1.1 Squamata. Snakes and lizards maintain this basic structure of the cloaca (e.g. Seshardi 1959), although the male reproductive apparatus is unique. All male squamates have a set of paired hemipenes situated at the base of the tail adjacent but caudal to the cloacal opening (e.g. Agrawal 1954). In some species of lizards the hemipenis is employed as a display structure during courtship and as such is often brightly coloured (Eberhard 1990). The hemipenes can have species-specific structures and in *Varanus* the penes are considered to be an important taxonomic tool for distinguishing species (e.g. Böhme 1988; Card and Kluge 1995; Bennett 1998). Female squamates have a hemiclitoris which can be partially everted, a structure that has been well documented in *Varanus* (King 1981a; Ziegler and Böhme 1996). At rest,

each hemipenis is stored in a sac and eversion is accomplished by muscular action and either vascular engorgement of blood sinuses or distension of lymphatic spaces. In its invaginated or resting state, the hemipenis consists of a blind ending tube lined internally by an epidermal epithelium with a spiral longitudinal groove. During eversion this groove lies on the outer surface of the erect hemipenis and becomes continuous with a groove, which originates inside the cloaca near the opening of the deferens ducts. Semen is conducted along the groove during copulation after which the hemipenis is returned to its storage sac via the action of a penis retractor muscle. In all squamate species, only one hemipenis at a time is inserted into the female's cloaca during copulation as the male alternates between hemipenes (King 1981a).

2.6.1.2 Crocodylia. The chambers of the crocodilian cloaca are kept separate by tight muscular sphincters. The largest chamber is the urodeum, whose epithelium is capable of water and ion exchange, thus serving as the primary site for postrenal urine modification (Kuchel and Franklin 2000). Both genders have paired gonads with the testis or ovary positioned along the ventro-mesial border of its corresponding kidney and connected via either a vas deferens or oviduct to the urodeum (King 1981a). The female reproductive tract is a long tube composed of seven distinct regions that begin at the anterior and posterior infundibulum, which receives ova from the ovaries, the *tuba uterine*, utero-tubal junction, the anterior and posterior uterus and terminates at the vagina which is connected to the urodeum (Palmer and Guillette 1992). These specialised sections have similar functions to the oviduct of birds, which will be discussed in detail below. The erectile unpaired phallus of the male is hidden inside the cloaca in its resting state. Located in the proctodeum, the phallus consists of a conical process of the anterior ventral cloacal septum. The basic structure of the phallus consists of a cylindrical, laterally compressed pair of joined connective tissue structures with a medial groove that extends dorsally to the anterior tip and serves as a passageway for semen. The tip of the phallus is comparable in structure to the mammalian glans penis and is distinct from both the protruding seminal groove fold and a blunt structure demarcated from the tip by a small ridge (Figure 2). Spongy tissue within the fibrous structures contains cavities which dilate and accumulate blood, though full eversion of the phallus from the cloacal folds requires addition support from muscular pressure (Reese 1915, 1924; Ziegler and Olbort 2004, 2007). Females have a clitoris which shares the location and general shape of the phallus, but it lacks a cartilaginous structure and is significantly smaller (Allstead and Lang 1995). Young crocodilians are commonly sexed via the insertion of a finger into the cloaca of an immobilised

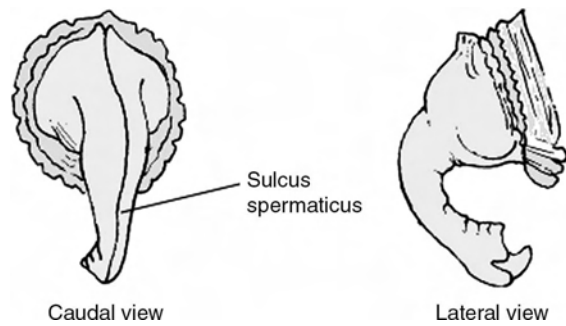


Figure 2. Comparative views of the crocodilian *C. palustris* phallus in both caudal and lateral views. Sketches after Kardong (1995).

individual to manually protrude either the phallus or clitoris, the former being more substantive with a distinctive conical structure (Brazaitis 1969). The phallus can also be manually protruded by the application of lateral pressure to the cloacal region along with a careful bending of the tail towards the crocodilian's underside (Whitaker et al. 1980). A less invasive technique involves simple visual examination of the internal cloaca of subadult crocodilians in which the phallus is purple and always much larger than the pink clitoris, growing at a rate 3–4 times faster (see Allstead and Lang 1995). It should be noted that the basic structure and layout of the crocodilian phallus is similar to that of the Chelonia, the primary differences being that the phallus of the former projects more prominently from the proctodeal wall when stored, is less dorsoventrally flattened and has a more elaborate glans. Both types of phallus employ a blood vascular mode of erection, are composed of two joined fibrous bodies and use a seminal groove to transport semen (King 1981a). The chelonian phallus furthermore demonstrates a remarkable convergence with the true penis of mammals in that both are reinforced by an axial orthogonal array of collagen fibres, a layout believed to maximally increase the flexural stiffness of the intromittent organ while resisting bending forces during coitus (Kelly 2002, 2004).

2.6.1.3 Aves. The cloaca of extant birds is divided into three separate compartments which maintain the essential functions observed in other reptiles. One notable difference is that the urodeum only receives products from the left side oviduct as the other is non-functional (King 1981a). The Apterygidae are the only group with two functioning ovaries (Sales 2005). All three compartments are kept separate by the coprourodeal fold between the coprodeum and the urodeum and the uroproctodeal fold between the urodeum and the proctodeum. The external vent of the cloaca is sealed by a muscular dorsal and ventral lip known as the labium venti dorsale and labium

venti ventrale, respectively (King 1981a; Soley and Groenewald 1999). The structural basis of the phallus offers no significant macroscopic difference to that of chelonians and crocodilians with a left and right fibrous body separated dorsally by a median seminal sulcus. The only substantive variation is that the avian phallus is asymmetrical with the left body larger than the right, which causes the shaft to bend noticeably towards the left (King 1981a). This unique deviation is likely associated with female birds having only one functioning ovary and may act to allow the bulk of ejected seminal fluid to be directed towards the urodeum's left oviduct opening. It should be noted that only about 3% of extant avian groups possess a true phallus, those being members of the paleognathae, Anseriformes and Cracidae, though despite that statistic their male genitalia are surprisingly diverse (Briskie 1998). The phallus itself is located on the ventral wall or floor of the proctodeum and among avians there are two distinct functional types of phallus: the true intromittent organs that are inserted into the cloaca during copulation and non-intromittent forms that do not physically penetrate the female but rather act to deposit semen directly onto the surface of her external genitalia, examples of which are demonstrated in Figure 3 (King 1981a; Briskie and Montgomerie 1997).

A typical example of a true intromittent organ is that of the male ostrich (*Struthio camelus*) whose phallus is attached to the ventral wall of the proctodeum where it is stored in a specialised phallic pocket. In its resting state, the organ is about 20 cm long as the shaft is bent in the middle on its ventral aspect when not in use. In its simplest form, the phallus comprises a conical shaft which consists of paired fibrous bodies. These are fused close to the base but separate near the tip to be joined by fibrous connective tissue, the left of which is longer and thicker, thus causing the direction of the erect shaft to deviate to the left. The dorsal groove between the fibrous bodies acts to form the phallic sulcus which originates at the papillae of the ductus deferens to terminate at the tip of the phallus. An elastic vascular body originates at the middle of the

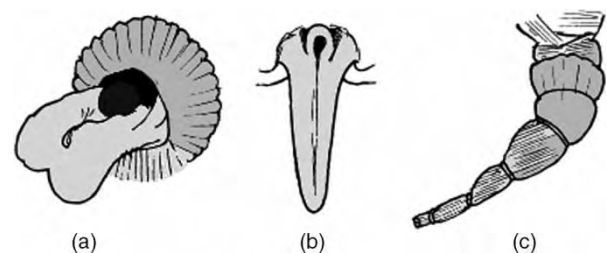


Figure 3. Genital organs of male birds demonstrating (a) the non-intromittent phallus of the domestic turkey and (b) the everted ostrich which in comparison is fully intromittent. The domestic duck phallus is shown in (c) its fully erect state. Sketches after Kardong (1995).

shaft and extends towards the distal end to form the phallic tip. This thick outer layer of elastic tissue works in conjunction with an inner core of erectile tissue to yield the elasticity responsible for both bending the flaccid shaft when stored and maintaining its ventral curvature when erect. There are two groups of muscles associated with erection and storage of the phallus. The levator phalli muscle is responsible for extruding the phallus from its storage pocket and maintaining the cranial redirection of the erect shaft. Two pairs of retractor phalli muscles withdraw the flaccid shaft into its resting position. The method of erection is decidedly different from other reptiles which rely upon blood vascular infusion and is instead believed to involve lymphatic engorgement. A large lymphobulbous phallus is situated on either side of the seminal groove which is directly linked to the somatic lymph system. When fully erect, the 40 cm long phallus projects from the cloacal opening in a marked ventrocranial curve, oriented slightly to the left with the phallic sulcus situated on its dorsal aspect (after King 1981a; Soley and Groenewald 1999). A similar phallic structure has been reported for other paleognaths, including the Tinamiformes (de Oliveira and Mahecha 2000) and the Apterygiformes (Caithness 1971).

Among the Neognathae, a well-developed phallic structure is present in all Anseriformes (King 1981a; Lake 1981), though the shaft tends to have a spiral, corkscrew-like appearance (see Figure 3(c)). The organ can be very long in relation to the male's size, an example of which is the Argentine Lake Duck (*Oxyura vittata*) whose phallus may be up to 20 cm in length and covered with series of bristle-like structures at the distal end. Female waterfowl have an equally long, corkscrew-shaped reproductive tract which spirals in the opposite direction to that of the male. These unusual genital arrangements are believed to be involved in sperm competition and female choice theories which will be discussed in further detail below (e.g. McCracken 2000; McCracken et al. 2001; Brennan et al. 2007).

There are unique variations of this theme such as the cloacal protrusion of the male Vasa parrot (*Coracopsis vasa* and *C. nigra*), which bears passing resemblance to the squamate hemipenis. The male's protrusion is formed by simple eversion of the cloaca and is inserted into the expanded cloaca of the female while the two copulate in a side-by-side position. It should be noted that while the protrusion is fully intromittent, it is not considered homologous with the phallus and is evolved independently (Wilkinson and Birkhead 1995). In that respect, Birkhead et al. (1993) noted that *Coracopsis* demonstrated much larger testis than expected in relation to body size and as testis size is known to increase along with the level of sperm competition (Møller and Briskie 1995), the protrusion is considered to have secondarily evolved as an adaptation to intense sperm competition in the species.

Non-intromittent phalli are a common feature of the reproductive systems of Galliformes and some passerines (Figure 3(a)). These structures bear passing similarities to true intromittent organs but are short and incapable of entering the female's cloacal opening. A pair of lymphatic folds originating from the proctodeum evert during sexual arousal to form a simple median furrow which acts to collect semen and position it on the surface of the female's engorged cloaca when mating (Briskie and Montgomerie 1997). In passerines the process of cloacal apposition is assisted by the eversion of a pair of conical papillae from the wall of the proctodeum (Birkhead and Hoi 1994) as intromittent capability was lost during evolution by continuing reduction of the ancestral true phallus (King 1981b). A unique attribute of male passerines is the cloacal protuberance which is a marked swelling of the cloacal region during the breeding season. This is caused by enlargement of both the seminal glomus at the terminal region of each deferens duct and an adjacent receptacle that opens into the cloaca through a flap of tissue called the papillae. This suggests that the sperm is temperature sensitive with the protuberance acting to keep the sperm in an environment that is cooler than the body's core temperature (Evans and Heiser 2004). The structure is diverse; as an example, the Fairy-Tail Wren (*Malurus cyaneus*) has a protuberance with a cartilaginous tip whose function remains unclear (Mulder and Cockburn 1993). It is not known why only male passerines maintain such a system though upon evaluation of cloacal protuberance anatomy, Møller (1988) and Briskie and Montgomerie (1992) noted that the size of both the protuberance and the testis was strongly associated with high levels of sperm competition.

Considering that 97% of male birds have no phallus, it has long been wondered why intromittent organs have persisted, as they are clearly not required for successful insemination and fertilisation of females. Most theories tend to invoke natural selection hypotheses, an example of which is that a phallus is required to prevent water from entering the cloaca in waterfowl during coitus, though that idea is negated by the fact that numerous aquatic species manage to successfully copulate on land. Furthermore, such an explanation simply cannot account for the loss of a phallus in almost every avian lineage (see King 1981b; Lake 1981). As the phallus is a secondary sexual character of males, modern hypotheses have focused on the influence of sexual selection theory and in that respect there are two distinct, though not necessarily exclusive, schools of thought.

The sperm competition hypothesis considers that an intromittent organ is more likely to increase the probability of paternity. This can be accomplished by allowing greater male control of the coital act, ensuring that ejaculates are placed directly inside the female reproductive tract and even displacing or diluting any

seminal fluids from previous matings (Birkhead and Møller 1992a). In that regard, the elaborate corkscrew patterns on the phallus of many birds strongly suggests a function involving either sperm removal or displacement (Briskie and Montgomerie 1997). Intromittent organ retention is prevented if male parental investment is low, whereas a high level correlates with the presence of a phallus. This idea was tested by evaluating division of parental care labour between males and females with the result being that males with a phallus invested heavily in both pre- and post-hatching care of offspring, while groups that demonstrated either female biased or female only care rarely had males with intromittent organs (Birkhead and Møller 1992a). When males have no intromittent organ, the female choice hypothesis notes that females then have the opportunity to either refuse sperm transfer or expel ejaculate soon after mating (e.g. Davies 1983, 1985; Davies and Lundberg 1984). It is therefore suggested that one would expect species with an intromittent organ more likely to engage in forced copulations, a prediction verified by the behaviour of waterfowl (e.g. McKinney et al. 1983; Coker et al. 2002). For sexual selection hypotheses to be workable, it is expected that intromittent organs will occur in taxa employing internal fertilisation which have either a high pre-hatching investment as predicted by female choice or considerable post-hatching male investment in offspring as predicted by sperm competition. In conclusion, both agents of selection may balance out or act in a reinforcing manner hence the importance of evaluating the costs and benefits of a phallus for both the male and female. It can be expected that an intromittent organ will be selected against and disappear altogether from a group when the costs exceed the benefits [see Birkhead and Møller (1992a) and references therein for a more detailed discussion].

In female birds, the left ovary is atrophied and it is only during the breeding season that it enlarges and becomes active. The ovary is suspended from the dorsal body wall situated ventral to the left kidney where it leads to the oviduct, a narrow tube-like structure that is composed of (1) the infundibulum, a fan-shaped structure that receives ovulated eggs from the ovary; (2) the magnum, which serves to produce the egg albumen; (3) the isthmus, where eggshell membranes are secreted; (4) the uterus, the wall of which is well muscled and (5) the vagina, containing sperm host glands and storage tubules which opens into the urodeum next to the opening of the left ureter (after King 1981a; Soley and Groenewald 1999). The reproductive tract of female birds differs dramatically from other oviparous amniotes in that the eggshell membranes and calcerous layer are produced in separate regions of the oviduct (see Figure 4). This is in contrast to most reptiles (including chelonians and lepidosaurs) and the monotremes where in both cases the oviduct or uterus secretes the membranes and

calcerous layer. The crocodilian oviduct employs similar specialised uterine regions, the isthmus and shell gland, which are ultrastructurally comparable to their avian equivalents and are considered homologous (Palmer and Guillelte 1992). This 'assembly line' morphology of specific regional tasks is unique to all extant archosaurs. However, one vital deviation is that avians can only ovulate one egg at a time, whereas crocodilians (as with other reptilomorphs) ovulate the entire clutch (Jones et al. 1979; Lance 1989). The archosaurian mode of egg production has further similarities in that patterns of yolk deposition in both birds and crocodilians bear striking similarity (Astheimer et al. 1989).

2.6.1.4 Implications for dinosaurs. There are no records of either reproductive tissues or genital structures being preserved in dinosaurs aside from the sole exception of eggs. However, the conservative nature of the reptilian cloaca throughout evolutionary history and the use of extant phylogenetic bracketing (e.g. Weishampel 1995a; Witmer 1995) can be employed to yield a plausible reconstruction. With the exception of placental mammals, the basic structure and functions of the three-chambered cloaca are a standard feature in all major tetrapod vertebrates including every extant archosaur and in that respect there can be little reason to doubt its presence in extinct archosaur groups. All male squamates, chelonians and crocodilians employ an intromittent organ, which is present in only a very small percentage of extant birds. However, the basic physical structure of the phallus is a pair of joined fibrous bodies with a medial seminal groove which is everted through the infusion of either blood or lymphatic fluid. The males of all crocodilians and paleognatha have a phallus which has been secondarily lost in the majority of neognatha. Furthermore, the only major structural difference between the crocodilian and avian phallus is that the everted shaft of the latter tends to have a left-hand directional bias and a lymphatic mode of eversion, in contrast to the blood vascular mode of erection in crocodilians and chelonians (see above discussion). Extant phylogenetic bracketing predicts the presence of a phallus in male dinosaurs and this conclusion is further supported by the size of large theropods and sauropods whose thick, heavy tails would have made the pressing together of everted cloacae (as in passerines) a physically impossible act.

As explained above, the oviducts of crocodilians and birds bear striking similarities in having an 'assembly line' mode of egg production with dedicated sections for the formation of albumen and shell. The only variations are that (1) birds produce and lay one egg at a time, whereas crocodilians deposit an entire clutch and (2) all extant birds with the sole exception of the Apterygidae have only one functioning left oviduct, whereas in crocodilians both

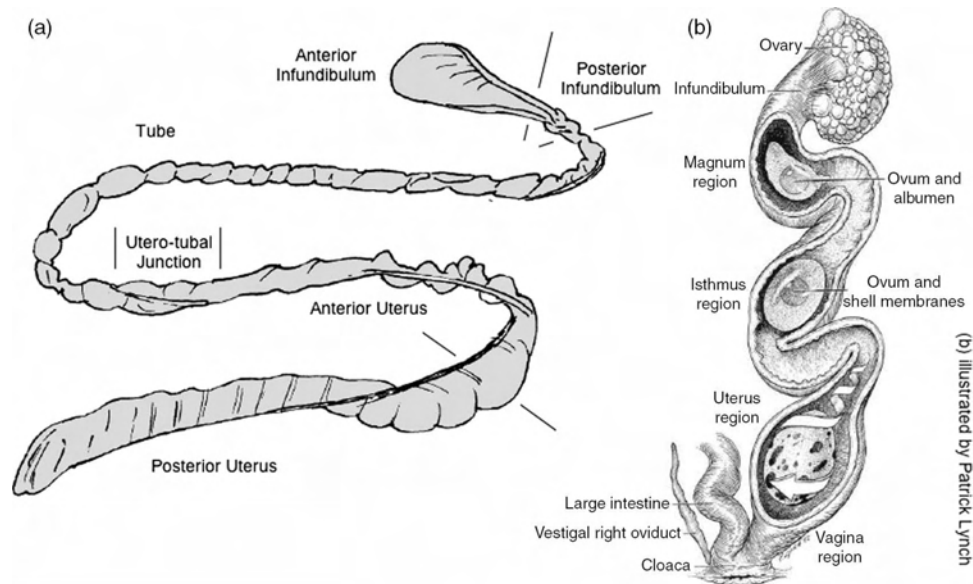


Figure 4. A comparison of the (a) crocodilian and (b) avian oviduct showing the homologous assembly line oviduct [left sketch after Palmer and Guillelte (1992) published by Elsevier; right from Proctor and Lynch (1993) and reproduced by permission of Yale University Press].

ovaries remain fully operational. The discovery of a possible pair of preserved unlaidd eggs in *Sinosauropteryx* (Chen et al. 1998) and confirmation of the same in an unknown oviraptorid species (Sato et al. 2005) provide demonstrable evidence that in theropod dinosaurs at least there was a unique amalgamation of both crocodilian and avian reproductive characteristics. There were clearly two functional oviducts like crocodilians, yet the number of eggs ovulated was reduced to one at a time per oviduct as in birds. The positioning of the eggs in the oviraptorid fossil further provides useful clues as to the most likely anatomical location of the cloaca which was estimated by Sato et al. (2005) as being ventral to the anteriormost caudal vertebrae.

Further insights regarding the female reproductive tract can be gleaned from the pathologies preserved in eggs, specifically the phenomenon of multiple eggshell layers. Female amniotes that produce hard-shelled eggs include some chelonians and all crocodilians and birds. These animals are known to exhibit abnormalities in their eggs in response to a variety of stress factors (e.g. Ferguson 1985; Solomon 1997). These are often caused by prolonged periods of egg retention in which the egg becomes stalled in the isthmus or shell gland where it receives either a second or more shells over the first, the result being a multi-shelled egg. In such a pathology the pores of the layers do not match, hence the developing embryo suffocates (e.g. Ewert et al. 1984; Carpenter 1999; Jackson and Varricchio 2003; Jackson and Schmitt 2008). Among fossilised dinosaur eggs, this condition has been well documented in a variety of eggshell types (e.g. Jackson et al. 2004) and appears

to be most commonly encountered in the megaloolithus type of eggshell structure which is known to be associated with sauropods (Hirsch 2001; Jackson et al. 2004; Garcia et al. 2006).

2.6.2 Models of tetrapod copulation and relevance to dinosauria

Frey (1995) convincingly demonstrated that in all non-mammalian vertebrates, there is a distinct and functional relationship between mating posture, length of intromittent organ and mode of locomotion. The mechanics of motion in the majority of non-mammalian vertebrates often involve a long and muscular tail, especially as a means of propulsion in crocodilians and lepidosaurs. A thick, large tail with a gradual transition to the trunk necessitates a lateral sexual position regardless of the presence of a single phallus or paired hemipenes. Animals with flexible trunks (e.g. lepidosaurs) engage in pronounced sideways bending of the body and tail to bring their reproductive organs into alignment and as such a long intromittant organ is not required. However, animals with more rigid trunks (e.g. crocodilians) can only copulate by means of either a modified sexual position or a relatively long phallus. During evolutionary history, changes in locomotion that yield significant reductions in tail length result in a corresponding modification of mating posture, with copulation then possible with the male mounting the female from behind as seen in both the chelonians and avians. Both the paleognatha and chelonians compensate for their having a rigid trunk by following a general trend

towards greater phallus length. Avians lacking a phallus overcome the rigid trunk in a variety of ways which include the male fluttering in place to maintain his position during copulation, a uropygium to allow for greater manoeuvrability of the cloacal area and by employing simultaneous eversion of the proctodeum of both genders (after Frey 1995). An evaluation will now be made concerning the copulatory behaviour of squamates, extant archosaurs and large-bodied mammals in an attempt to ascertain the apparent usefulness of mating posture models in regard to dinosaurs.

2.6.2.1 Squamata. The copulatory behaviour of the Lacertilia fits well into the above model of mating posture with one notable exception, the horned lizards *Phrynosoma platyrhinos* and *P. coronatum* which have been observed to copulate in a ventral position (Tollestrup 1981). The copulation of lace monitors (*Varanus varius*) has been well documented both in the field and in captivity and in that regard serves as a useful general model for the sexual behaviour of Lacertilia. The female lies still flat on the ground while the male approaches from the rear and to one side. With his snout pointed down towards the female, he rapidly moves his head from side to side as he tongue-flicks across her back and neck. He proceeds to mount her laterally in a position in which his body lies across her diagonally so that his head is brought up to the right side of hers and his cloaca adjacent to the left side of her tail. The male swings his right hindlimb over the base of her tail and uses his claws to scratch at the right side of her tail. This stimulates the female to raise the base of her tail and recurve her back, in the process lifting her hindquarters off the ground and arching her tail. Using his right foot to hold her securely in place, the male then curves the base of his tail underneath hers and inserts the right hemipenis into the female's cloaca (see Figure 5 for an illustration of this posture). Approximately half a minute after insertion the male initiates a series of methodical thrusts driven primarily by his left hindlimb for about a minute after which copulation is terminated. The accumulated time from initial approach of the male until withdrawal spans about 2–3 min (Carter 1990).

Observations and recordings of captive *V. varius* copulation closely follow the above account, though Dr D. Kirschner (personal communication) noted that the male's thrusting behaviour only occurs during the latter part of mating; for example, if intromission lasts from 3 to 4 min, thrusting will only occur during the last minute or less. Several minutes later the pair copulate again, with the male approaching from the other side to employ his left hemipenis and this mode of alternating from left to right each mating continues for up to and over an hour, with 16 to 18 copulations per session (Carter 1990; Kirschner, personal communication). It should be noted that among varanids,

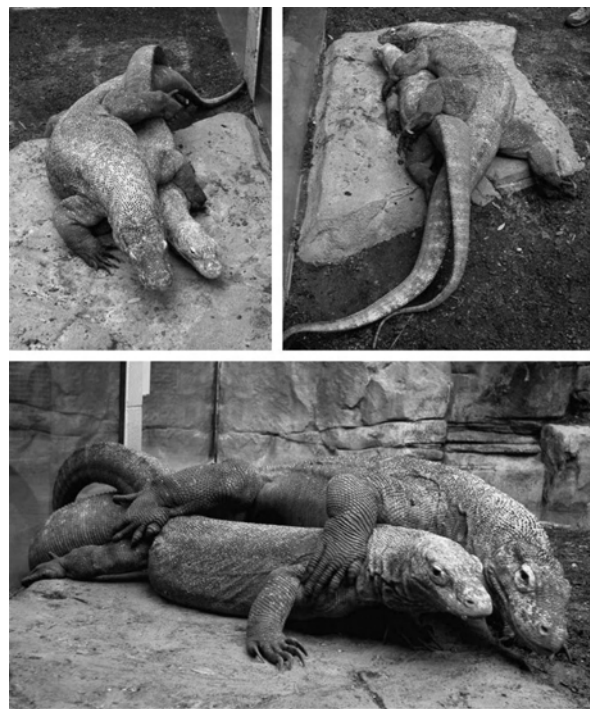


Figure 5. Copulation posture of Lacertilia as demonstrated by Komodo Dragons (*V. komodoensis*). Photographs courtesy Judith Bryja, Houston Zoo.

this prolonged mating period appears to be unique to *V. varius* and may be due to sperm competition factors (Carter 1990). Despite this variant, the mode and posture of mating is little different from that described in the varanids *V. komodoensis* (Auffenberg 1981), *V. bengalensis* (Auffenberg 1983, 1994), *V. timorensis* (Moehn 1984), *V. olivaceus* (Auffenberg 1988), *V. rosenbergi* (King and Green 1993), *V. niloticus* (Hagen et al. 1995) and for numerous other lizard species (e.g. Vestal 1940; Rodriguez-Dominguez and Molina-Borja 1998). Mention should be made of the Sphenodontia, a sister group of the Squamata which includes the tuatara (*Sphenodon punctatus*) in which the larger dimorphic male copulates employing direct cloacal apposition (Mlot 1997; Lutz 2005). The flexible trunk of Lacertilia is unlike the more rigid vertebral structure of the dinosaurs and the further presence of truly unique hemipenal structure appears to disqualify lizards for use as sexual posture models. However, the 'leg over back' method of mating is by no means unique to this group and in that regard provides a valuable and useful insight.

2.6.2.2 Crocodilia. The sexual behaviour of crocodilians is not an easy subject for study as the entire process occurs underwater, often in a murky and turbid environment where underwater visual recording is either unworkable or too dangerous. There have been reported incidents

of terrestrial copulation (e.g. Yadav 1969; T. Crutchfield, personal communication), though evaluation of the very few photographs taken (courtesy C. Manolis, N. Whitaker and V. Dinets) shows that the animals are not in copulation but rather the male is simply positioned on the female's back with her cloacal area pressed against the ground while his lies either directly against or lateral to her sacral region. A sexual position similar to that previously described for monitor lizards was noted by V. Dinets (personal communication) for a captive pair of *Crocodylus palustris*, though unfortunately the behaviour was not recorded. It should be noted that reports of terrestrial copulation attempts appear to be observed exclusively in captivity when either water levels are low or when a large number of animals are crowded into a pool. The behaviour does not appear to have been documented among crocodilians in their natural habitats (J.A. Calderon, personal communication).

Vliet (2001) noted that in the wild, copulation of *A. mississippiensis* was achieved by the larger male mounting the back of the female upon which he would secure his position by clasping her with his forelimbs. He uses a hindlimb to balance his weight while sliding off to one side so that his tail can be rotated under that of the female. The male's phallus is extruded from the cloaca with a notable semicircular bend towards his ventral surface (Ziegler and Olbort 2004, 2007), whose orientation likely helps locate the female's vent. The male then moves his tail forward and in response the female raises her tail slightly up and towards the male to assist with alignment of their genitalia so that insertion can occur (Vliet 2001). Each vaginal canal of the distal oviduct opens separately into the cloaca (Palmer and Guillette 1992), though it is not known if these structures physically extend into the urodeum during sexual arousal and/or subsequent intercourse to physically receive the distal end of the phallus.

A similar mating technique was noted by McIlhenny (1935) in a pair of wild penned alligators, although there are differences reported for duration of intromission in this species. Vliet (2001) noted matings of approximately 30 s, Joanen and McNease (1971) 5–7 min and McIlhenny (1935) stated 10–15 min, though this is likely due to individual variation. Copulation can occur many times daily over a period of several days (McIlhenny 1935) and multiple paternity has been well documented (e.g. Davis et al. 2001). The modified dorsolateral posture has been reported in many other species (e.g. Staton and Dixon 1977; Steel 1989; Kofron 1991), though there are a few variations. The sexual position of *Caiman crocodilus* is related to water depth and when at low levels the female mounts the male so that her body is angled over his back and tail inverted beneath his, presumably to locate and receive the phallus (Alvarez del Toro 1974; Staton and Dixon 1977).

Furthermore, J.A. Calderon (personal communication) noted that among *Caiman c. fuscus*, female mounting of males during copulation occurs when the number of females greatly exceeds that of males. This observation suggests that the behaviour is related to female competition over a limited choice of potential mates. Finally, Kofron (1991) noted two additional postures in *Crocodylus niloticus* which appear unique to either the species or study population. One of these positions has the female mounting the male in the standard crocodilian manner as noted in *Caiman* and in the other, the pair is stationed belly to belly with the male covering the female.

Accounts of crocodilian sexual behaviour at both zoological parks and captive breeding centres are little different from those described above (e.g. Legge 1967; Whitaker and Whitaker 1977; Tryon 1980; Widholzer et al. 1986; Alcalá et al. 1987; Diaz et al. 1990; Trutneau and Sommerlad 2006) with the modified dorsolateral mating posture common across all species (e.g. see Figure 6). In conclusion, crocodilians fit in with the aforementioned functional morphology arguments of Frey (1995) in that their relatively rigid trunk only allows for copulation to occur via a modified sexual position in comparison to Lacertilia. The preference for an aquatic medium for copulation and anatomical differences would at first glance appear to eliminate the crocodilians as a potential model for dinosaur mating reconstructions. However, much like the lacertilians, crocodilians employ the familiar 'leg over back' mounting technique to counter

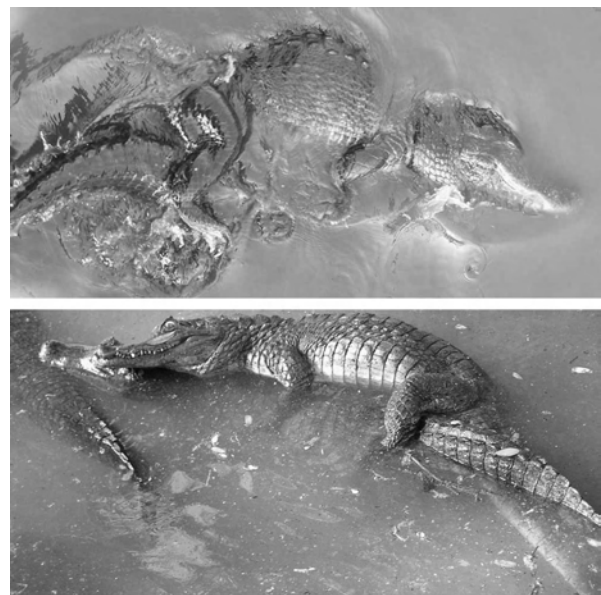


Figure 6. The mating posture of (above) the American Alligator (*A. mississippiensis*) and (below) Spectacled Caiman (*Caiman crocodilus*) is typical of crocodilians. Photographs courtesy Vladimir Dinets.

the presence of a thick tail. This may represent either a convergent behavioural solution to a common problem or an artefact of their shared diapsid ancestry.

2.6.2.3 Aves. Birds mate with the male mounting the female in a dorsolateral manner with the only substantive differences apparently based on body size, presence of a phallus and whether cursorial or volant. Copulation in the Paleognathae has variants, but is generally little different from what has been observed in the ostrich (*S. camelus*). There are some minor variations in the described courtship behaviour of the ostrich, but in general terms the process begins with synchronised ground pecking by both genders as they feed close together. Eventually the male walks towards and around a pre-chosen nesting area and initiates an elaborate display by throwing his wings upwards, alternating between left and right during which the white wing feathers are conspicuously flashed. He then drops to the ground, the continuous rhythmic side to side beating of his wings causing dust to whirl each time a wing tip brushes across the ground. All the while, he repeatedly twists his neck from side to side in a manner that resembles a continual corkscrew motion (Sauer and Sauer 1966). Males were frequently observed to evert their phallus during courtship displays (Sauer and Sauer 1966) in a similar fashion to the everted hemipenes of certain courting male lizards (e.g. Eberhard 1990), though this behaviour has not been reported in some ostrich studies (e.g. Bolwig 1973).

An interested female responds to the male's display by walking with her head lowered, tail drooping and wings pointed down in a curve. The moment she lowers herself to the ground, the male rises and rushes towards her with both wings still flapping. He mounts the female by placing a foot on each side of her body while craning his neck slightly backward to press his chin against his now fluttering throat. The male then lowers himself chest first so that he rests on top of her and in this position he resumes his former side to side rocking movements, swinging his neck from side to side as he attempts to locate the female's cloaca with his everted phallus. During his initial attempts at insertion, the female holds her head high and remains passive, though once intromission is accomplished she lowers her head and proceeds to swing her outstretched neck from side to side, pecking randomly at the ground. During copulation, the male bends his head forward, continuing to sway it from side to side although now at half its former speed, while at the same time he pokes his bill at the female's left and right clavicular region. His wings stop their rhythmic beating to be held horizontally where they quiver vigorously in a vertical plane. After an intromission of about 40 s, the female abruptly rises to her feet, pushing off the male, after which the two separate though mating may be repeated 50–55 min later (after Bolwig 1973).

Among other paleognatha, a variation in mating posture has been described for the Greater Rhea (*Rhea americana*). Courtship behaviour is similar to that of ostriches, in that the male rhea uses his wings as a primary display platform. He walks towards potential mates with both wings held open and forward to display both his body and everted phallus, frequently lowering both wings so that the wing tips are dragged along the ground. When a female is ready to copulate, she sits down on her tarsi in front of the male and rests her abdomen on the ground. The male responds by positioning himself so that he also sits on his tarsi directly behind her and while grasping the feathers on the back of her lower neck with his bill proceeds to initiate a series of strong thrusting movements (Codenotti and Alvarez 2001). When a female Emu (*Dromaius novaehollandiae*) is ready to copulate, she crouches in front of the male who then positions himself behind her. In a sitting position, the male gradually moves towards her tail until his legs are placed on either side of the female upon which he partially everts his phallus. As he raises his chest to attempt cloacal contact, the female pushes her abdomen back and everts her cloaca. The male moves further forward and continues to raise his body until intromission is achieved, at which point the phallus becomes fully everted and erect. During intromission, the male grasps the back of the female's neck until he ejaculates and dismounts, whereupon his phallus gradually invaginates to return to its proctodeal pouch (Malecki et al. 1997).

Most members of the Neognathae, which include passerines and virtually all other living birds, have no phallus. Copulation involves eversion and subsequent juxtaposition of both the male and female cloaca which are then briefly pressed together to facilitate transfer of sperm, an act colloquially referred to as the 'cloacal kiss' (e.g. McCracken 2000). During intromission, the male maintains his precarious balance on the female's back by securing her neck, snout or cranium in his jaws, rapidly fluttering his wings and holding onto her back or sides with his feet (Figure 7). As has been discussed, female birds have only a left functioning ovary and associated oviduct with entry to the latter located on the left side of the urodeum. It has been noted that when mating, the males of many avian species will preferentially mount and enter females from the left side (e.g. Gerhardt 1933 in King (1981a, 1981b); Petersen et al. 2001; Nyland et al. 2003), presumably to deposit sperm as close as possible to the oviduct opening, although Nyland et al. (2003), cautioned that this might also be related to lateralisation of the avian brain.

2.6.2.4 Large Mammalia. Mammals have a very different evolutionary history from dinosaurs and as such clearly cannot be used for studies involving extant phylogenetic bracketing. However, their body plans may



Figure 7. Typical copulation posture employed by birds, e.g. (a) Tree Swallow (*Tachycineta bicolor*); (b) Muscovy Duck (*Cairina moschata*) and (c) Lapwing (*Vanellus vanellus*). Note the male frequently employs his bill to grasp the female's neck feathers which helps him maintain his dorsoventral position. Photographs from Wikipedia Commons with credit to (a) Ken Thomas, (b) Ianare Sevi and (c) Mirko Thiessen.

provide some insights into putative sexual postures in dinosaurs and in that respect the mating behaviour of a few select mammals will be examined in detail. At first glance, the Rhinocerotidae appear to be a useful model as they bear a passing resemblance to the ceratopsids in terms of overall build and gait.

All species of rhinoceros have a pair of lateral projections located between the tip and middle of the penis that are flaccid when relaxed. When the penis is erect, these flaps protrude laterally as much as 20–25 cm to become firm and slightly cupped. Unique to both the Rhinocerotidae and Tapiridae, these lateral penile flaps are species-specific in shape and when inside the vagina act to significantly increase the diameter of the erect penis (see Cave 1964; Schaffer et al. 2001). It has been suggested that these structures serve as a locking mechanism of sorts (Zahari et al. 2002) and further support for this idea was offered by Buechner and Mackler (1974) who observed that despite the female slowly moving about while mating, the male had no difficulty in maintaining full insertion of his penis. Rhinoceros sexual behaviour has been well documented in captivity and in the field with no noticeable difference. There is little in the way of courtship documented among rhinoceros species beyond basic contact behaviours, olfactory exploration and pressing of the chin by the male onto the female's perineum to test her willingness to be mounted. Copulation begins with the receptive female responding to a male's advances by standing still, whereupon he makes an initial attempt at mounting. The male moves forward to rest his lower jaw on the female's rump and using his chin as a pivot, he subsequently pushes forward and with his hindlimbs placed wide apart, he then lifts both forelimbs onto the female's rump while anchoring his chin firmly on her sacrum. The male then uses his forelimbs to 'row' forward onto her lumbar region at which point an initial attempt at penetration is made (Zahari et al. 2005).

Evaluation of videofilm describing both attempted and successful mating in the Indian rhinoceros (*Rhinoceros unicornis*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*) and Northern white rhinoceros (*Ceratotherium simum*

cottoni) all follow the above behavioural routine for the initial mount of the female with little variation. Once the male is mounted as described above, he begins to repeatedly lift his erect but downward pointing penis towards the female's vulva and during each of these initial attempts at penetration, he may perform a series of quick thrusts. It often takes a fair amount of time for the male to locate the vulva and after each unsuccessful 'penile lift', the penis drops back towards the ground and the cycle continues. Should the male position himself too far forward on the female's back, his penis will either pass beneath her or laterally and in such instances the male may abort a mount to try again. In some behavioural sequences, the female appears to facilitate his repositioning by moving forward slightly so that he is mounted in a manner that allows for eventual penile contact. Considering that the shaft may be up to 1 m in length, there is evidence that the male must learn how to properly place himself on the female at this stage of mating and in that regard practice may be necessary (e.g. see Buechner and Mackler 1974). Some males in captivity have never been observed to effectively mount a female despite being housed together over long periods (Dr K. Carlstead, personal communication).

Eventually the distal end of the penis successfully locates and penetrates the vulva, whereupon the male will 'row forward' with his forelimbs. He continues to drag his brisket along the lumbar region of the female until he is fully mounted and in doing so inserts the length of his penis into her vagina, finally, securing himself by resting his forelimbs just behind her shoulder folds (e.g. Goddard 1966; Zahari et al. 2005; Figure 8). Video sequences demonstrate that at this point in the mating, the male may undertake a few movements in which he uses a combination of pushing with his hips and pulling with his forelimbs to pull himself as far up her back as possible and perhaps optimise the depth of penetration. Once fully mounted, the male begins very brief bouts of vigorous pelvic thrusting (about 4–6 s) that occur at intervals of between 2 and 4 min and at the end of each session ejaculation occurs. The duration of intromission is

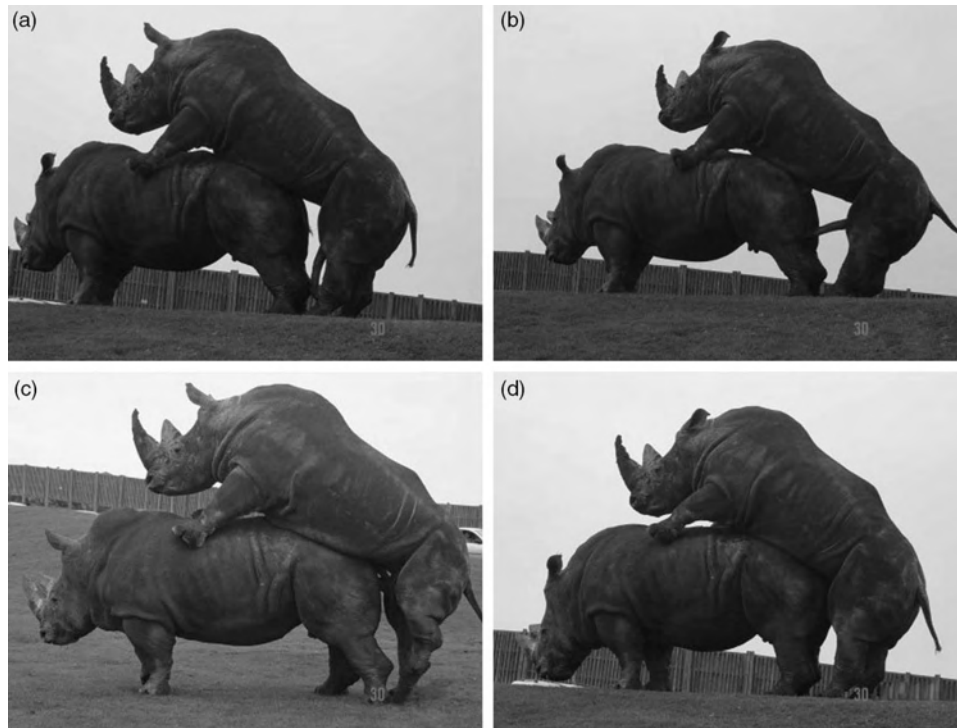


Figure 8. Rhinoceros mating sequence showing (a) the male mounting with penis erect; (b) performing penile lifts; (c) achieving vaginal insertion and (d) in full copulation. Photographs courtesy of the West Midland Safari and Leisure Park, Worcestershire, UK.

variable, though Buechner and Mackler (1974) reported matings that lasted up to 60 min. The male dismounts in a similar fashion to mounting, moving back along the female's lumbar region and using his chin to gradually lower both forelimbs to the ground.

The sexual behaviour of the Elephantidae is perhaps most notable due to the presence of a highly mobile penis which one might theorise had an equivalent in the larger species of dinosaur to assist with genital alignment and insertion. The overall structure of the elephant penis follows the standard mammalian model and is retractable with the testicles housed internally. Movement of the erect penis is controlled by a pair of large dorsally situated levator penis muscles that are positioned anteriorly just below the ischial arch and attached to the dorsal surface of the penis. The two levator muscles unite with the compressor venae dosalis to form a common tendon that inserts on the dorsum of the corpus cavernosum penis which acts to maintain the S-shaped flexure of the erect penis (Short et al. 1967). It should be noted that the levator penis has a fleshy attachment point at the tuberosity of the ischium (Schulte 1937). The retractor clitoridis muscle in the female is similar in location and size to the retractor penis of the male. It arises from the coccygeal vertebrae and passes backwards and downwards to its insertion point in the strong fascial layer overlying the urogenital canal in the anal region. The levator clitoridis muscle, analogous to the levator penis of the male, also originates from the

ischium where it inserts to a powerful tendon and forms a prominent cord extending along the dorsum clitoridis to the anterior tip of the clitoridis (Perry 1953). These muscles work together during copulation in that when the male hooks the upwardly flexed tip of his penis into the female's ventrally located vulva, she retracts the penis both caudally and dorsally using the levator clitoridis which allows the male to insert the full length of his penis (Short et al. 1967). The penis itself is reported to weigh up to 27 kg and reach up to 1.5 m in length (Sparks 1977).

There is no courtship behaviour documented among the Elephantidae and a receptive female will respond to the approach of a male by remaining still while she shifts her tail slightly off to one side and carefully moves her hindlegs apart in a wide stance (Slade 1903; Kuhme 1963; Kingdon 1979). The male positions himself directly behind the female and mounts her by first swinging his head over her rump to gently place his trunk and tusks lengthwise on her back. Lifting one forefoot then the other, the male uses his tusks for leverage as he rises on his hindlegs. He places his forelegs on the female's flanks while he sinks down on his hindlegs into a near sitting position, likely to help keep at least some of his weight off her back in addition to bringing their genitals into alignment. To compensate for the reduced mobility of the hindlimbs and sacral joint of male elephants, the penis is under full voluntary control. When fully erect, the tip of the penis becomes swollen and assumes a marked

S-shaped flexure. Instead of thrusting with his pelvis, the male uses the highly mobile penis, moving it vigorously from side to side and up and down in the vertical plane to probe for the female's vulva which has been turned backwards by erection of the clitoris as described above. Once the tip of the penis locates and penetrates the urogenital sinus, insertion is accomplished via a series of rapid up and down motions of the penis (Figure 9). Upon successful insertion, the male then partially raises on his hindlegs and instead of thrusting with his pelvis, he uses the muscular action of the penis to move it inside the female's urogenital tract. Intromission lasts for between 30 and 90 s and after ejaculation, the male lowers himself to the ground by more or less reversing the mounting procedure, withdrawing his penis in the process (e.g. see Buss and Smith 1966; Eisenberg et al. 1970; Kingdon 1979). There appears to be little variation in copulatory technique between the various species, though one minor

note is that while most accounts accentuate that no pelvic thrusting occurs during intromission, this behaviour has been noted in the field by both Slade (1903) and Douglas-Hamilton and Douglas-Hamilton (1975).

Large, heavy terrestrial mammals that might act as templates for putative dinosaur sexual behaviour copulate in a dorsoventral posture with the male mounting and entering the female from behind (Sparks 1977; Wallace 1980) though there are some exceptions. The family Phocidae includes both species of elephant seals in which sexual dimorphism is extreme. A full grown male northern elephant seal (*M. angustirostris*) averages 4.5 m in length with an average weight of 2275 kg, while females by comparison average 2.95 m and 513 kg. The difference is even more marked in the southern elephant seal (*M. leonina*) with mature males reaching an average weight of 3510 kg and an average length of 4.67 m compared to the female's average measurements of 503 kg and 2.7 m, respectively (Alexander et al. 1979). Unlike the Rhinocerotidae and Elephantidae, all pinnipeds have a baculum, a bone that apparently provides added rigidity to the penis, though its precise function remains controversial (Lariviere and Ferguson 2002). While the habitat and predatory niche of *Mirounga* is decidedly aquatic, the animals can only copulate and give birth on land.

The massive weight and size of the male elephant seal in comparison that of the female makes the dorsolateral mating stance unworkable. Therefore, copulation is assumed in a modified lateral position. There are no substantial differences between either species of *Mirounga* in regard to sexual behaviour and posture nor is any form of courtship present. The male moves directly to the side of a receptive female who is lying prone on her belly and places a foreflipper over her back. He then firmly pulls her towards him and makes an initial attempt at establishing genital contact. A co-operative female remains passive, indicating her willingness to copulate by first lifting her perineum into a lordotic posture then spreading her hindflippers. The male then shifts his weight from his belly to his side and positions himself so that his penis is in relative juxtaposition with the female's genital area. Only the distal tip of his penis is extruded as the male probes for the vulva, though many of these initial attempts at penetration fail. Occasionally, the male thrusts forcefully and his penis may extend to its full length of 41–46 cm to pass underneath, over or lateral to the female before being withdrawn to the distal tip. Insertion is successful when signalled by an especially deep pelvic thrust, the result of which is an externally noticeable flexure of the lumbar region of the male's spine. Full extension and tumescence of the penis occurs with intromission, at which point the male will pull the female towards him at half minute intervals while simultaneously pushing his pelvis forward. During the last half of copulation, the female assumes the active role, with mild undulations slowly passing through

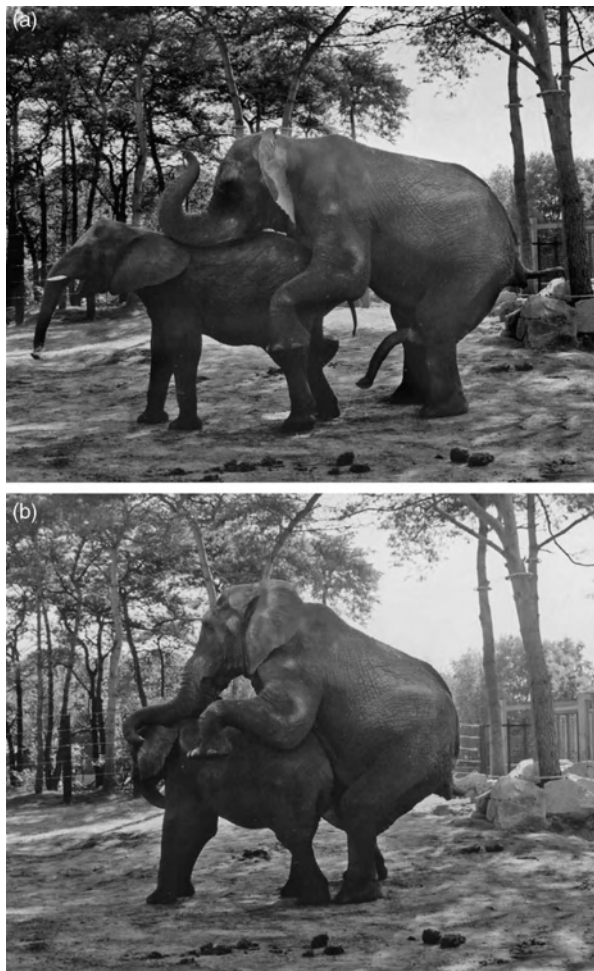


Figure 9. Copulation of elephants showing (a) initial mounting by the male and flexure of his mobile penis followed by (b) location and subsequent penetration of the female's vaginal orifice. Photographs courtesy Hans Orbons, Safaripark Beekse Bergen, The Netherlands.

the posterior region of her lower trunk during which she gently extends and flexes her hind flippers (Figure 10). She elevates her perineum and slowly moves her body back and forth which acts to slide her vagina over the penis. Copulation lasts between 3 and 10 min to terminate by either the male or female moving away from the other (Bartholomew 1952; Laws 1956; Leboeuf 1972).

Such modified sexual postures are not unique to terrestrial mating species of the Phocidae. Among marsupial mammals, the common wombat (*Vombatus ursinus*) employs a mating posture similar to that of elephant seals. The male rolls the female onto her side and mounts lying partly on his side at a right angle across her hindquarters. During copulation the male is situated behind his mate with his hindlegs on one side of her and front legs on the other (Triggs 1996; Marks 2005; Hughes and Hughes 2006). The Macropodidae are capable of bipedal locomotion, and even though the tail is used as a tripod when at rest their copulatory posture deserves evaluation. There is very little difference recorded in regard to the mating technique used among the *Macropus* species. A receptive female kangaroo presents to the male by crouching with her back arched whereupon he proceeds to mount, standing semierect behind her and clasping her so that his forearms are tucked inside her thighs. He mounts slightly to one side of her midline with one foot placed on either side of her tail, a posture that enables the male to place his erect penis inside her urogenital sinus.

Intromission is accomplished during a short sequence of thrusts as the male pulls the female back onto his penis. There is little activity during copulation, though every few minutes the male initiates several strong pelvic thrusts in quick succession with ejaculation occurring after a duration of between 10 and 25 min (after Sharman and Calaby 1964; Dawson 1995). To prevent further mating with other males, a post-mating plug which drops out after a few days is formed in the female's urogenital sinus (Poole and Pilton 1964).

2.6.2.5 Putative coital postures for dinosaurs. With regard to extrapolating the most parsimonious mating postures that might have been employed by dinosaurs, a variety of models of both related and unrelated forms have been reviewed which include the usual suspects of the extant archosaurs in addition to large, heavy mammals such as the elephant and rhinoceros. Unfortunately, the sexual postures of extant birds are of very little use in relation to acting as possible models for dinosaur mating behaviour, for although a small minority of birds have phallic structures, they have no tail to obstruct access to the female's cloaca. The situation is further confounded by the use of cloacal apposition as the primary avian means of copulation, a position that was not physically possible for dinosaurs to achieve. Crocodilians are of equally limited use as they have a very different gait and limb structure from dinosaurs and furthermore reply upon being

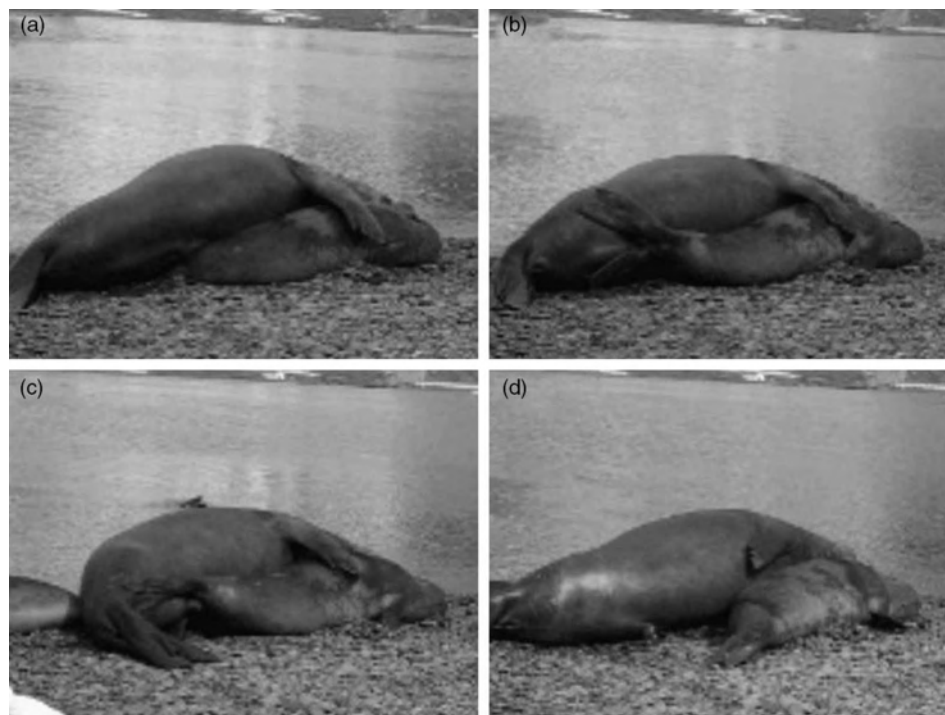


Figure 10. Elephant seal mating sequence showing (a) initial mounting by the male; (b) preliminary attempts at penetration; (c) insertion of the penis and (d) withdrawal and termination. Captures from videofilm provided courtesy Sarah Lurcock.

submerged in an aquatic environment to counter weight distribution during intromission, a sexual prerequisite which would likely have been untenable for most, if not all dinosaurs. While there have been a few claims made of crocodilian terrestrial mating with the male covering the female, there has never been any unequivocal, definitive visual documentation recorded of this alleged behaviour.

Extant archosaurs thus provide few tenable clues as to how their extinct relatives may have mated and, unfortunately, mammals fare little better. Both elephants and rhinoceros lack a thick, heavy tail and have their genitalia positioned quite differently compared with dinosaurs, in which the cloacal region was located behind the pubic boot just underneath the tail (e.g. Sato et al. 2005). Moreover, the highly motile penis of the elephant is controlled by muscles that attach to the pelvic bones and despite extensive reviews of the archosaurian pelvis (e.g. Hutchinson 2001; Langer 2003), there remains no indication of attachment points or scars that might have supported an equivalent structural layout in dinosaurs. The reproductive area of extinct archosaurs appears to be located further back under the tail than in male kangaroos whose 'tail straddling' behaviour during copulation does not appear to be workable in dinosaurs. The modified lateral mating postures of elephant seals and wombats clearly demonstrate that there are alternatives to the standard dorsoventral method of coition; however, variations of this method would likely be problematic for many dinosaurs, especially in large, heavy species due to the pressure applied to the ribcage and lungs when lying on one side.

The earliest attempts to describe the possible mechanics of dinosaur sexual behaviour were offered by Halstead (1975), who suggested that there was no male intromittent organ and in the absence of same advocated the use of an avian 'cloacal kiss' model of coition. This idea envisioned the male's cloaca, set back beneath the tail, becoming engorged with blood and bulging out to penetrate and fill the opposing cavity of the female. It was suggested that all dinosaurs used the same basic mating position with the male always keeping one foot on the ground when mounting to keep his weight from inflicting any crushing injury to his mate. The female would squat down with her tail raised and twisted to one side while the male proceeded to mount from the rear, placing his forelimbs across her shoulders and one back leg over her hip before twisting and pushing his tail underneath hers so that their cloacae were in direct physical contact (Halstead 1975; Fritz 1988). Ideas involving both lack of an intromittent organ and direct cloacal contact during intromission have by no means been completely abandoned and continue to attract proponents (e.g. see Amalfi 2005; Fernandez 2008).

The problem with the 'no phallus, cloacal contact' hypothesis has been alluded to above but deserves more

detail. Among extant archosaurs, a male phallus is demonstrably ubiquitous among crocodilians, paleognaths and some neognath groups, and the organ shares an identical basal structure and proctodeal origin (see Figure 11 for a comparative distribution). Many male dinosaurs would not have been able to replicate the tight twisting of the tail required for Halstead's (1975) sexual posture reconstruction due to the extensive stiffening of the dinosaur tail. The tails of many saurischian theropods maintained their rigidity by a number of long, thin bones and cartilage, an adaptation likely related to the need for a counter-balance during bipedal locomotion (Carpenter 1999). Furthermore, a similar phenomenon is found in the Ornithischia, a defining character of which are the ossified tendons that occur along the vertebral spines of the back and tail whose function is poorly known. The ancestral state is that of a longitudinally arrayed lattice of tendons along the spinous processes of the vertebral column which, in their derived condition, become ossified and increase spinal stiffness. It is thought that increasing the stiffness of the tail influences locomotion by firmly anchoring muscles to the tail which act to allow a more powerful contraction of the hindlimb by reducing ventral flexion of the tail during muscular contraction. Ossified tendons may also have served as a storage medium for elastic energy throughout the gait cycle and for the maintenance of a horizontal vertebral column (Organ 2006). Clearly this rigid back and tail effectively prevents a male ornithischian from twisting or coiling his tail around that of a female to augment copulation in the manner employed by lacertilians.

As has been previously discussed, both the flexible trunk and unique hemipenial structures of lacertilians

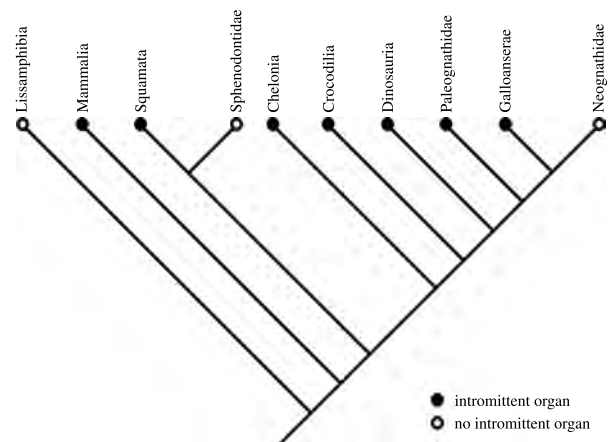


Figure 11. The phylogenetic distribution of intromittent organs in the amniotes would strongly indicate that a penis-like structure is a synapomorphy for amniotes with independent losses in both the Sphenodontidae and Neognathae, although it is alternatively possible that intromittent organs were a convergent trait (cladogram inspired by Kelly 2002, 2004). This study would strongly indicate that a phallus is ancestral to the Archosauria to be lost in the Neognathae.

would appear to completely eliminate the group as a reliable model. However, the 'hindleg over tail' technique of achieving genital juxtaposition with an intromittent organ is also employed by crocodilians. Both groups share this solution to the mechanical problem of how to successfully bring together the male genitalia and female vent despite the problem of having a thick tail. This particular copulatory method further appears to fit the functional association theory postulated by Frey (1995) and noted above. Therefore, the best generalised model for mounting behaviour in dinosaurs appears to be a variation of the standard reptilian 'leg over back' posture to facilitate copulation. For the majority of dinosaurs, it is hypothesised that the female would assume a lordotic posture as seen in the Felidae (e.g. Tefera 2003) by first leaning forward so that her hips and tail are elevated before moving her tail off to one side to make her cloaca both visible and accessible. The male would proceed to mount from behind and slightly to one side of the female's midline with one foot on the ground as he swings his other hindlimb over her hips and tailbase, supporting and steadying himself by placing his forelimbs on her back. At this point the female might even lower her hindquarters slightly should it make it easier for her partner to raise and place his hindleg over her. With their cloacal regions now in relative alignment, the male could use his hindleg and forelimbs for both added grip and leverage while carefully manoeuvring his hips and hindquarters in a manner so that the distal end of his extruded phallus locates and penetrates the female's cloaca (see Figure 12(a)–(d) for hypothetical mating postures). Based on extant archosaurs, it can be surmised that copulation was likely brief and may have been repeated over a set period of time. It is interesting to note that a similar copulatory technique was independently arrived at by Carpenter (1999, 2000) with the added idea that more advanced theropods, such as *Sinosauropteryx*, may have mated using an avian style 'cloacal kiss' while other dinosaurs retained the crocodilian phallic structure (Carpenter 1999).

Objections might be raised to such a sexual position in regard to the weight applied to the female's back. However, when copulating a male rhinoceros mounts so that his forelegs reach the female's shoulders so that the bulk of his weight is pressed directly on her back with no consequent damage. When in a mounted position, the hindlimbs of both a male and female dinosaur would carry much bigger loads than when standing at rest. When a male lifts one hindlimb, the other limb has to carry twice the standing load and if the leg is placed over the female's back, her hindlimbs would carry an increased load. However, these loads would be no greater than those experienced during walking, when the peak forces on the feet were likely about twice as high as in simply standing. In effect, if dinosaur skeletons were strong enough to withstand the forces of walking, then they should be strong

enough to allow for the rigours of sexual positioning (after Alexander 1989). In further regard to skeletal strengths, Tanke (1989) noted that hadrosaurs from Alberta, Canada, were occasionally found to have broken proximal to mid-caudal neural spines with subsequent rehealing. The more distal caudal neural spines demonstrated a rapid decrease in the frequency of pathologies towards the end of the tail. It was suggested that injuries to the proximal caudal spine were related to damage inflicted during sexual behaviour and that skeletons with such traits were likely to be female. It is most likely that female hadrosaurs copulated while on all fours with tail lifted and held slightly to one side as proposed by the 'leg over back' hypothesis. In such a position some of the male's weight would have most certainly rested directly upon the female's tail base and in particular the tips of the neural spines. It is therefore possible that accidental injury to the female's basal tail spine may have occurred while the pair positioned themselves for initial mounting or during intromission itself. Lambeosaurines have more elongate chevrons and much taller caudal neural spines than other hadrosaurids and in that respect may have been more prone to such injuries. While there may be a more simpler explanation, this scenario appears a reasonable hypothesis (Tanke 1989; Rothschild and Tanke 1991).

While the proposed 'leg over back' posture appears to be workable as a general hypothetical model, there were undoubtedly variations to this theme among dinosaurs. The possible mating habits of the Thyreophora have long been the subject of conjecture with the rows of plates, spines and armour that characterises this group apparently conspiring to render copulation unworkable. Carpenter (1999) suggested a female *Stegosaurus* might simply squat in the front while standing on her hindlegs in a manner similar to that described above, while the male rests his forelimbs on one side of her broad pelvis. However, while such a position might allow for a theoretical mount by the male while on two legs, it does not explain how their reproductive organs could be made to connect. A lack of penile control muscle attachment scars has already been demonstrated and no dinosaur fossil, regardless of preservation quality, has ever been found with a baculum or equivalent structure. Considering the distance between both male and female cloaca in a pair of *Stegosaurus* with the male mounted on two legs, a phallic structure would have to exit his cloaca, negotiate around the pubis and then rise upwards to meet and penetrate the female vent. Such a lengthy and curvilinear organ would undoubtedly have required some means of a support configuration, but there is nothing to be gleaned from anatomical evaluations to fit such a purpose.

Among mammals, both the old world (Hystriidae) and new world (Erthizontidae) porcupines have hair that is modified into sharp spines, but are able to successfully copulate in the standard dorsoventral manner. When

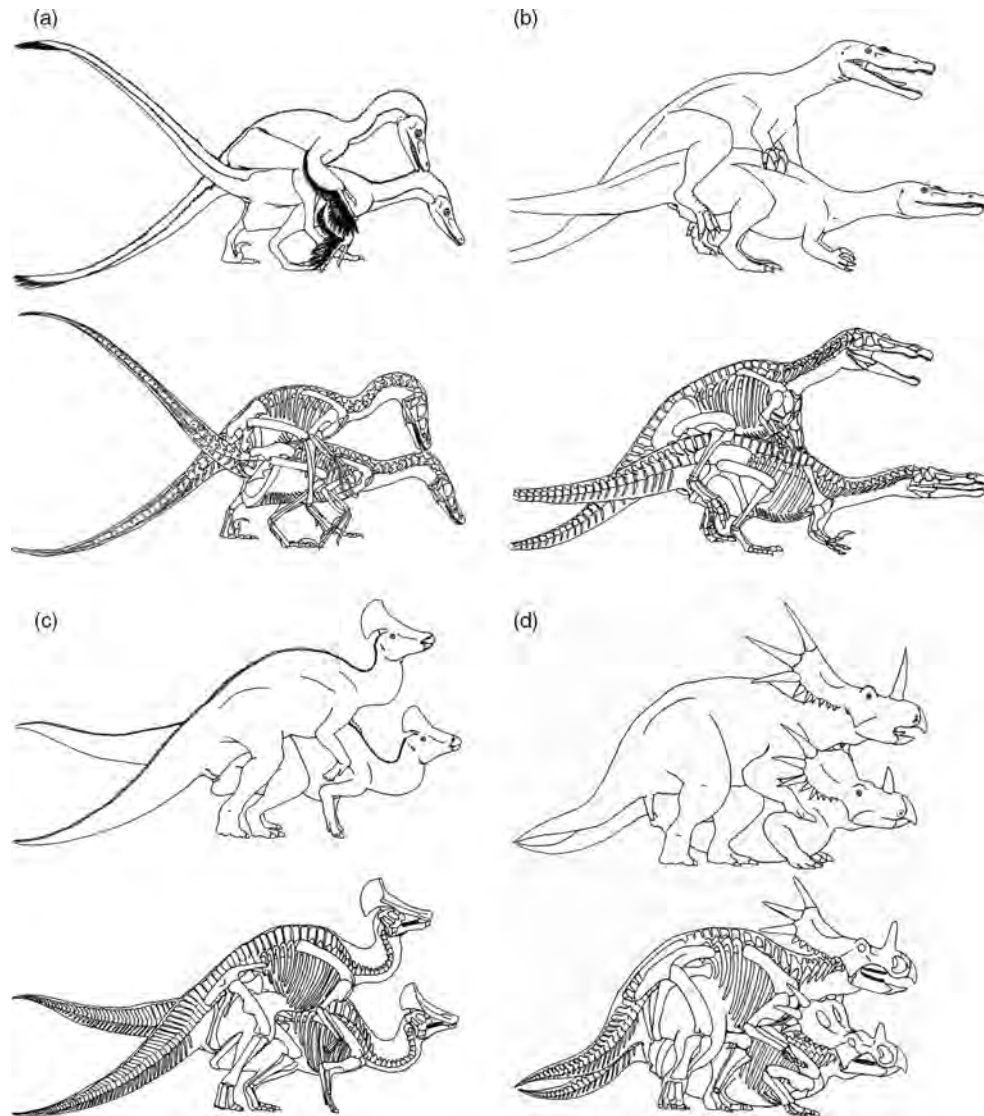


Figure 12. Putative reconstructions of sexual postures for (a) small theropod *Velociraptor mongoliensis*; (b) large theropod *Baryonyx walkeri*; (c) hadrosaur *Olorotitan arharensis* and (d) ceratopsid *Styracosaurus albertensis* presented in both skeletal and life restorations.

a female is receptive to mating, she lifts her hindquarters slightly and raises her tail, the underside of which has no spines, to curve it up and over her back. This covers her dorsal spines and stretches back her hindlimbs so that her genitalia are exposed to the male. Approaching from behind, the male rears up and walks on his hindlimbs to mount, covering her so that his ventral surface is pressed against the underside of her tail. To further avoid her spines, he does not clasp her with his forelimbs as he proceeds to insert his penis. During the 2–5 min intromission, he performs a series of thrusts by repeatedly flexing and then straightening his knees with copulation terminated by a simple dismount (Shadle 1946; Shadle et al. 1946; Felicioli et al. 1997). Thyreophora cannot move their dorsal plates (e.g. de Buffrenil et al. 1986) and the structure of the vertebral column clearly does not allow

for such contortions, both of which render the porcupine model irrelevant. It has been proposed and illustrated by Bakker (1995) that copulation in *Stegosaurus* may have been accomplished with the female lying on one side while the male mounts from the rear, resting his forelimbs on her hips while he crouches to insert his phallus. The hypothesis is certainly original and would have made the female's cloaca accessible in addition to the obvious implications for sexual positioning in *Spinosaurus* and other 'sailbacked' dinosaurs. Unfortunately it would not work for such related genera as *K. aethiopicus* and *L. durobrivensis* due to the presence of a backward projecting spike arising from each shoulder (Carpenter 1999). It may be speculated that these two animals mated by standing in a relative 'back to back' manner, with the female assuming lordosis and remaining stationary while the male

manoeuvred his phallus into her cloaca. Many stegosaurid forelimbs were dramatically shorter than the hindlimbs (e.g. Galton 1990) with the result being a tail held high off the ground, an anatomical quirk that may have been a catalyst for the adoption of such a unique copulatory method (see Figure 13).

Sauropods include the largest known terrestrial vertebrates to have ever lived (e.g. Upchurch et al. 2004) and how such truly massive creatures managed to achieve any form of sexual intercourse remains unknown. There has long been controversy regarding the issue of whether sauropod dinosaurs were capable of adopting a bipedal or tripod stance using the tail as a prop or 'third limb' to extend their effective feeding range. The restoration at the American Museum of Natural History (New York, NY, USA) of the sauropod *Barosaurus* rearing up on its hindlegs is a good example of the tripod hypothesis. Landry (1992) raised a series of objections to the *Barosaurus* reconstruction, arguing that the physics of such behaviour would have required muscles of a cross-sectional area of at least 1.4 m^2 to produce the necessary force. No muscles of such size are apparently available that could produce the force required to lift the animal's weight. Moreover, concern was raised over the consequences of the kinetic energy absorbed by the foreleg bones produced by the animal's weight dropping down from a 5 m height. This concern was echoed by Rothschild and Molnar (2005) who noted that if sauropods were to on occasion adopt a bipedal stance, then one might expect to find evidence of stress fractures in the metacarpals and associated bones of the forelimb hand, none of which have been found. Landry (1992) further argued that the total stresses of the vertical compressive load would act to crush the vertebral column and a sudden doubling of the hydraulic column imposed upon the venous return to the heart causing problems with cardiac output.

Landry (1994) revisited the problem of bipedal stances in large sauropods, arguing that such activity would place an intolerable strain upon the venous return to the heart which would likely have resulted in congestive heart failure. This controversy is related to the overall function of the sauropod neck and whether it was regularly held in an upright posture. If so there would be the expected requirements of both an extremely high arterial blood pressure and the presence of a very large heart (Seymour 1976; Seymour and Lillywhite 2000). Possible solutions have involved multiple accessory hearts arranged in a series (Choy and Altman 1992) and a gravity-driven siphoning mechanism in the neck (Badeer and Hicks 1996). Rejecting both hypotheses, Seymour and Lillywhite (2000) concluded that sauropod end-diastolic and stroke volumes were likely far smaller than previously assumed, with smaller stroke volumes requiring correspondingly smaller hearts that would either beat faster or reduce the blood flow rate. An erect neck may have been possible if sauropod metabolism was lower than that of endotherms. Upchurch and Barrett (2000) referenced the structure of the cervical intervertebral joints as mechanical evidence to support the ability of neck raising and furthermore suggested that the neck may have been lightened by air-filled sacs in the cervical pleurocoels that would have acted to lower the mean tissue density. However, in terms of feeding, articulated reconstructions of *Apatosaurus* and *Diplodocus* would indicate that their necks were held relatively straight and at a gentle inclination so that the head, already positioned at a downward angle relative to the neck, was close to ground level. This would imply that for at least some sauropods, a preferred strategy of ground feeding and low level browsing was the norm as opposed to high browsing (Stevens and Parrish 1999). However, this view has been challenged by Taylor et al. (2009), who demonstrated that

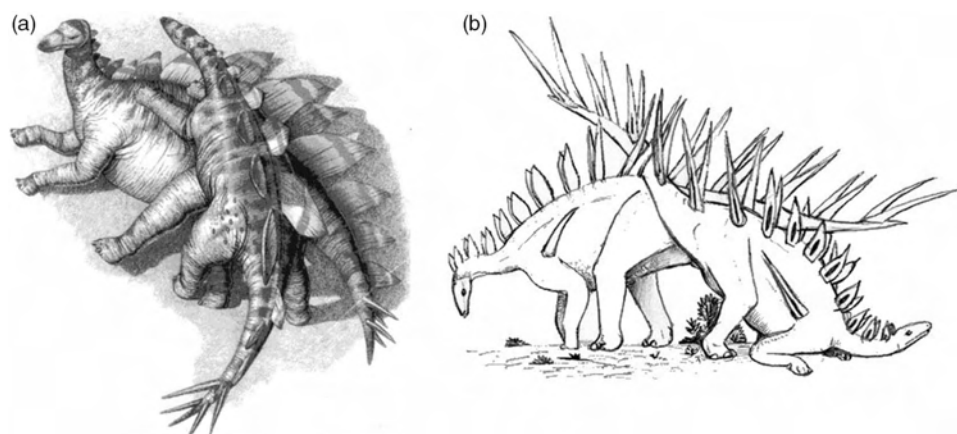


Figure 13. Putative sexual positions for the stegosaurid taxa (a) *Stegosaurus* and (b) *K. aethiopicus* demonstrating how intromission could have been accomplished despite the presence of their respective ornamentation. Sketch (a) is used by permission of Patrick Redman and (b) is courtesy Brad McFeeters.

in sauropods the neck was extended and the head flexed using modelling based upon inferences from extant amniote groups.

Many sauropods are known to have had a shortened dorsal vertebral column, short forelimbs, high sacral neural spines, a centre of gravity located near the pelvis and a lengthy, strong tail. Together, such traits strongly suggest that rearing up on hindlimbs fell within the biomechanical range of workable behaviours for these animals (see Alexander 1985, 1989; Choy and Altman 1992; Upchurch et al. 2004). Moreover, it stands to reason that male sauropods must have been able to rear up at the very least to allow for the successful mounting of the female during the initial stages of copulation. A possible solution would be for sexual behaviour to take place in a submerged aquatic environment to take advantage of the neutral gravity, a scenario also recognised by Landry (1994) who noted that a mounting male sauropod would have to support about 10–20 tonnes in a rather precariously stable position 2–3 m off the ground. There is now consensus that sauropod species were fully terrestrial based upon a wide range of ecological, biomechanical and sedimentological lines of evidence (see Bakker 1971; Coombs 1975; Alexander 1985) and further opposition to the aquatic mating hypothesis may rise from possible confounds involving the mechanical work of breathing when the torso is submerged under several metres of water (Kermack 1951; Dennis 1992; Taylor 1992).

However, such concerns regarding the collapse of the lungs and airways in response to submergence in water have all been based on the assumption that sauropods were dense enough to sink to the bottom of a body of water. Henderson (2003) employed computer models that incorporate the basic physics of buoyancy and equilibrium to study how bodies react when immersed in water. Sauropods have a highly pneumatized axial skeleton and system of thoracic and abdominal airsacs that both act to reduce their density to about 80% that of water. Computer models indicate that the animals would likely have ridden high in the water and thus have been rather unstable, floating so high that a *Brachiosaurus* in 4.7 m of shoulder deep water would not have been able to reach the bottom with its hindlegs. Indeed, the longer forelimbs of both *Brachiosaurus* and *Camarsaurus* would have allowed them to propel themselves by walking along the bottom with hindquarters floating free, a scenario that fits well with the widely distributed manus-only trackway sites described by Coombs (1975), Ishigaki (1989) and Lee and Huh (2002). In contrast, other sauropods such as *Apatosaurus* and *Diplodocus* were found to have likely floated, with their forelimbs higher than their grounded hindlimbs. When all four limbs float free from the bottom, the animals become highly unstable and thus susceptible to capsizing, hence there would have been great difficulty in swimming. Further evidence that supports at least the

occasional aquatic incursion by sauropods can be gleaned from their trackways found along both marine intertidal zones and the muddy margins of lakes (e.g. Lockley 1991) which sedimentological evaluation indications were created when the area was covered by water (Pittman 1989). The conclusion is that sauropod dinosaurs could have submerged and walked in water at the very least as deep as their chest height (Henderson 2003; Stokstad 2003).

The above lines of evidence make the aquatic mating hypothesis a workable possibility which leads to the question of just how the largest and heaviest of sauropod species might have copulated. A rare attempt at reconstructing the sexual behaviour of these animals was seen in the 1999 BBC television documentary series, *Walking With Dinosaurs*. A pair of *Diplodocus* were shown to mate employing a mammalian dorsoventral position with the male mounting the female from behind and to the side of her tail, while keeping both his feet on the ground. While not shown, in such a position it can only be assumed that the male presumably used a motile intromittent organ to locate and thus penetrate the female's vent. Such a sexual position would not have been possible considering that the dorsoventrally thickened tail would have kept the cloaca far apart. In a stereotypic mammalian mating stance, the sheer distance required for an intromittent organ to bridge both the male and female cloaca, in addition to allowing for a depth of penetration suitable for effective delivery of semen, would have required a phallus of considerable length. As previously discussed, there are no lines of evidence that would suggest either the presence of a baculum-style support structure or the muscular attachments needed to control a highly mobile phallus.

In contrast, the aquatic mating hypothesis model will now be discussed using *Brachiosaurus* as a chosen model. It can be speculated that a receptive female would enter a body of water to shoulder height with the male approaching from behind, whereupon he would mount by rearing up so that the weight of his chest and placement of his forelimbs would act to push the female's floating hindquarters to the ground. With the female stable on all four limbs, the standing male would proceed to place a hindlimb over her tailbase in the standard 'leg over back' posture, this being more parsimonious as it would allow for closer juxtaposition of both the everted phallus and cloacal opening. At this point, it is important to recall the fusion of the caudal vertebrae previously described for sauropods in detail and thought to be a female trait based on its uneven distribution. It can now be clearly seen how this modification would have allowed the female's tail to be moved in the slightly upward and sideways arching motion that would have made her cloaca more accessible to the male in addition to maintaining the rigidity of her tailbase during intromission. Securing himself with his

forelimbs and manoeuvring his hips, the male would then guide the distal end of his phallus towards her vent and upon insertion the organ itself would act to stop water from entering the female reproductive tract as in crocodilians (Figure 14). Aquatic mating would have undoubtedly mitigated problems of weight distribution for the larger sauropods although the smaller, less heavy species and many prosauropods were likely able to successfully copulate terrestrially using the standard 'leg over back' technique. It is perhaps interesting to close by noting Carpenter's (1999) suggestion that by the time some sauropods reached maximum size, they may have been already well past their reproductive years.

Now that the most likely mode of copulation and subsequent fertilisation have been hypothesised and described for dinosaurs, it may be useful to examine the phenomenon of sperm storage. Among extant reptiles, oviductal sperm storage has been documented in the females of all taxa with the exception of the Amphisbaenia, though it remains poorly studied in the Rhynchocephalia. Specialised sperm storage tubules (SSTs) evolved separately in the Chelonia and Squamata. These structures are located in the distal half of the oviduct and occasionally in the uterus of the chelonians. The ancestral condition for squamates is for SSTs in the uterine tube though more derived squamates such as iguanids and *Anolis* have evolved vaginal SSTs which, in the latter, are more similar to those of birds (after Sever and Hamlett 2002). In chelonians, stored sperm appears most likely to be used for fertilising eggs ovulated during the second and subsequent clutches (Gist and Congdon 1998). Davenport (1995) reported that likely sperm storage in the caiman (*Paleosuchus palpebrosus*) and recent investigations have confirmed its presence in the American alligator (*A. mississippiensis*). Histological examination of two regions of the alligator oviduct identified as containing sperm in the lumina of the oviductal glands, one at the junction of the posterior uterus and vagina and the other at the junction of the tube and isthmus. The glands of the former junction reacted weakly when tested for proteins and carbohydrates, whereas the latter junction reacted positive for both products which are associated with sperm storage structures in other reptiles. Oviductal sperm storage was

found in both recently mated females and those associated with a nest with the conclusion that female alligators can store sperm in their oviductal glands but only for a single breeding season (Gist et al. 2008; see also Bagwill and Sever 2006, 2007). The utero-vaginal junction of birds contains SSTs, the number of which tends to be correlated with the amount of sperm per ejaculate. Duration of sperm storage was found to have a slight yet positive correlation with clutch size and a stronger positive relationship with the number of days in which oviposition occurred (Birkhead and Møller 1992b). Clearly, such an investigation is not possible in regard to dinosaurs but the presence of sperm storage capabilities in most reptiles, including both groups of extant archosaurs, may suggest the ability for extinct relatives.

Recent research has cast new light onto questions concerning the possible timing and onset of sexual maturity in dinosaurs. In extant squamates and crocodilians, sexual maturity begins with an initial slowing of growth rates as adult size is approached. By contrast, extant birds initiate sexual behaviour and ensuing reproduction well after somatic maturity. By counting growth lines and related spacing in the bones of all seven species of theropod dinosaurs found preserved in association with nested eggs, an attempt was made to determine which stage of development each specimen had attained before death. It appears that in theropods, sexual maturity occurred well before the adult size was reached in a manner similar to the ancestral reptilian condition which strongly indicates that the overall life history and physiology of theropod dinosaurs were decidedly different from that of extant birds (after Erickson et al. 2007). This observation was replicated in a series of growth curve reconstructions conducted by Lee and Werning (2008) which revealed that reproductive maturity in *Allosaurus*, *Tyrannosaurus* and *Tenontosaurus* coincided with a transition from growth acceleration to deceleration. Despite fairly rapid growth, once again the dinosaurs studied proved more similar to reptiles as sexual maturity developed before adult size was reached. It was further proposed that early reproductive maturity in growing individuals suggested they were relatively precocial at hatching and probably experienced a high rate of adult mortality.

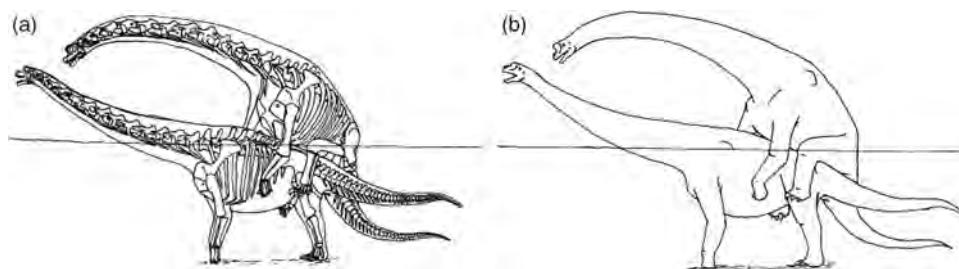


Figure 14. Putative restoration of sauropod *Brachiosaurus* aquatic copulation with both (a) skeletal and (b) life restoration.

2.6.3 Nesting patterns and parental care

A dearth of sauropod eggs inspired some investigators to suggest live birth as a reproductive option for these animals due to the width of the pelvic canal (e.g. Bakker 1986; Morell 1987). This scenario was countered by the discovery of fossil beds containing a significant number of sauropod eggs and embryos (e.g. Chiappe et al. 1998, 1999). Among extant reptiles, viviparity has evolved at least 100 times among the Squamata (e.g. Andrews and Mathies 2000), but has never appeared in the chelonians, birds and crocodilians, which may reflect physiological and morphological constraints that became established in their distant evolutionary history. The simplest model for oviparity considers a gradual increase in the length of time an egg is retained in the oviduct during which development proceeds at an optimal rate. The embryos of the latter groups are not capable of developing beyond a very early stage while in the oviduct due to the heavily calcified eggshell and the resultant limited exchange of respiratory gases that can occur. The situation is further complicated by the presence of a thick eggshell of which any reduction would adversely effect the mineralisation of the embryonic skeleton (see Packard et al. 1977; Andrews and Mathies 2000). The need for oviposition to occur at a relatively early stage of development has thus acted to limit the reproductive options of all living archosaurs, and extant phylogenetic bracketing indicates a similar obligate oviparity for their extinct relations.

The eggs of crocodilians and birds share numerous similarities that include a thick, hard shell composed of calcite crystals pierced by numerous pores to allow for the diffusion of respiratory gases. The shock-absorbing albumen is kept separate from the eggshell layers by a pair of tertiary shell membranes. However, in contrast to avian eggs, those of crocodilians have neither an air space for the initial inflation of the neonate's lungs nor chalazae to anchor the growing embryo in place and thus allow the egg to be manually rotated by the parent (Packard et al. 1977; Carpenter 1999). Another key difference is that the gender of a developing crocodilian embryo is determined strictly by the nest temperature during incubation as in chelonians (e.g. Ferguson and Joanen 1982; Paladino et al. 1989). In both mammals and birds, gender is genetically fixed by heteromorphic sex chromosomes (e.g. Standora and Spotila 1985), though it is not known as to which strategy the various genera of dinosaurs employed considering the difficulty in testing any such hypothesis. The eggshell of the theropod *Troodon formosus* demonstrates many similarities to that of birds that include prismatic shell units and a squamatic ultrastructure, both considered to be unique avian shell traits. In total, there are 15 egg and shell characteristics that are believed to be either shared or convergent, which suggests a similar mode of reproductive physiology (Varricchio et al. 2002;

Varricchio and Jackson 2004a). Further avian traits include the eisospherites and their associated fibres that attach to the basal region of the mammillae and the radiating crystal formation of the spherulites that grade into the wedge-like structure of the mammillae. However, the dual squamatic and mammillary layers within the eggshell are believed to be either an apomorphy of theropods or arisen within the group. The external eggshell layer of crown group avians is likely apomorphic in comparison with the eggshells of theropods, a condition which strongly suggests that the prismatic ultrastructure evolved independently in both the Neognathae and Troodontidae (Zelenitsky et al. 2002). Dinosaur eggs tend to be associated with certain taxonomic groups and in that regard are frequently classed into parataxonomic groups (Hirsch and Zelenitsky 1997), a brief example of which is the megaloolithid egg type specific to sauropods (Chiappe et al. 1998). However, it should be noted that Zelenitsky and Therrien (2008) reported that many high level parataxonomic categories are not monophyletic, suggesting that the offending groups be abandoned with the oofamily level being considered sufficient.

Both eggs and nests of dinosaurs have been discovered across the globe, although the majority of finds are from Upper Cretaceous strata in Argentina, Mongolia, France, India, China and the United States (Carpenter and Alf 1994). Suitable soil conditions such as drainage and pH levels were apparently important control factors in regard to the distribution of dinosaur nest traces and embryonic material (Carpenter 1982). The nest structure of crocodilians and birds has been previously discussed and as a summary, the former is either vegetation mounds or excavated holes, while that of the latter tends to be much more varied. One extant nest type deserves particular mention, that being the Megapodidae which bury their eggs in large mounds of vegetation and earth with incubation reliant on decomposition, geothermal activity and solar ambient heat. There is no rotation of the eggs, the young are superprecocial and therefore there is no post-hatching parental care (Jones et al. 1995). This has previously been viewed as a possible primitive condition for birds and thus perhaps for dinosaurs (e.g. Coombs 1989; Larson 1998), though Jones et al. (1995) made the point that these unique features are an autapomorphy of the Megapodidae and therefore it would be unwise to employ this highly specialised group as a general model for dinosaurs.

Clutches and linear patterns appear to be the two primary egg laying strategies that were employed by dinosaurs. The former can be further divided into three distinct groups based upon the nest shape and the distribution of eggs, which can be laid in concentric circles, inverted cones or spirals. By contrast, in the latter group, eggs can be arranged in either parallel rows or arcs. Among titanosaur sauropods, three different nesting and

oviposition patterns have been reported. In the first type, 6–8 eggs in a circular pattern are laid in random distribution into a nest that is conical in cross-section and likely excavated by the forefeet. A variant of the conical nest type is a rounded shallow pit containing 3–6 eggs. There is evidence of possible colonial nesting in that nests appear to be close together, though it is not known if this was the result of one laying female or more. The second nest type consists of a pair of eggs deposited not in clutches but rather in arcs which, if connected, would form circles of a 1.3–1.7 m radius containing between 15 and 20 eggs. It is suspected that these arcs may directly correspond to the turning radius of a laying female. These unique arcs of eggs are not isolated but rather found in overlapping groups and on occasion clutches of 6–8 eggs can be found between these circles, though it is not known if they are meant to act as a predator lure or decoy. The third and rarest nest type is that of eggs arranged in four or five linear rows. The relatively thick eggshell of titanosaurs may have been an adaptation to either a lack of nest guarding or as a means to minimise damage to the egg during oviposition (Moratalla and Powell 1994).

A nest trace of the ornithischian *Maiasaura* was described at the Two Medicine Formation of Montana by Horner and Makela (1979) as an excavated bowl shape containing the remains of 15 individual metre-long juveniles. The nest itself was thought to be composed of mud and measured 2 m in diameter with a depth of about 0.75 m (Horner 1984; Moratalla and Powell 1994). There is a degree of controversy regarding whether Horner and Makela (1979) actually found a nest or simply an association of juveniles. The original inference of a nest was based upon a small lens of green mud stone embedded within beds of red mudstone which was interpreted as evidence of a nest structure. However, whether differences in colour substrate can be used as an adequate criterion for the recognition of putative nest traces has been questioned as such colour differentiation can be the result of secondary sedimentary processes. Rather, fossil nests are best recognised on the basis of substantive textural differences between the host substrate and the overlaying deposits (after Grellet-Tinner and Chiappe 2004). Nevertheless, this particular find would later play a role in the controversies concerning parental care in dinosaurs, a discussion of which will be forthcoming. The crater-like nests of the basal ceratopsid *P. andrewsi* were described by Brown and Schlaikjer (1940), though upon reviewing the evidence, Thulborn (1992) suggested that the original nest descriptions more likely represented those of hadrosaurids. It was proposed that a more feasible nest structure for *Protoceratops* was one composed of a shallow radial array of eggs concealed beneath a fairly low mound of soil, with the resulting low profile more parsimonious for such a low slung animal (Thulborn 1992).

Colonial nesting has been previously noted for both crocodilians (e.g. Cott 1961) and birds (e.g. Elphick et al. 2003). The many advantages of this strategy include increased vigilance for the presence of predators and the aforementioned dilution effect. There have been several lines of evidence that this behaviour may have been present in extinct archosaurs. Based on taphonomic evidence, Weishampel et al. (2000) suggested that *Protoceratops* were not only highly gregarious but also nested communally. Evidence of substantial group activity from both bonebeds and trackways have resulted in suggestions that more advanced ceratopsians not only lived in large herds, but may have possessed relatively complex social organisations (Sampson 1995a, 1995b) which may also have even included females nesting in groups. The Rio Colorado Formation in Argentina extends across several kilometres and contains an extraordinary number of sauropod egg and nest traces leaving little doubt that these animals were highly gregarious during the nesting season (Chiappe et al. 1999). Colonial nesting on a beach was suggested by Sans et al. (1995) during an evaluation of a site in northern Spain; however, this was later refuted by Sander et al. (1998) based upon re-evaluation of sedimentological evidence, though support was found for long-term site fidelity. Perhaps the best known suggestion of colonial nesting was presented by Horner (1982, 1984), who described *Maiasaura* nests that were approximately 7 m apart, about the proportions of an adult. This conclusion was strongly questioned by Carpenter (1999) who considered the offered evidence to be an artefact of erosion rather than that of behaviour. The lack of marker layers (e.g. a covering of ash) made it impossible to reliably separate one year from the next or demonstrate that the clutches were laid at the same time. To date no discovery has been made to indicate that theropods engaged in any type of communal nesting behaviour.

One unique nesting strategy observed in extant avians is that of brood parasitism in which females lay their eggs in nests constructed by other bird species or hosts who thus assume full responsibility for the incubation and subsequent provisioning of the parasite's young. This relieves the parasite of any parental duty and is a well-known strategy of both the North American Cowbird (*Molothrus* spp.) and European Cuckoo (*Cuculus canorus*). In contrast to interspecific parasitism, many birds practise intraspecific parasitism which occurs when a gravid female's nest is destroyed or compromised, whereupon she will seek out a nest of her own species to deposit her developing egg (after Alcock 1989; Elphick et al. 2003). A possible example of brood parasitism in dinosaurs was reported by Norell et al. (1994), who described a weathered nest of oviraptorid eggs from Ukhaa Tolgod in Mongolia that contained not only an oviraptorid embryo, but also two tiny dromaeosaurid skulls including

one preserved with an eggshell fragment still adhered. It is plausible to speculate that a female dromaeosaurid may have deposited a pair of eggs during a period when the oviraptorid nest was unguarded, though whether this behaviour was opportunistic or obligate is not known.

Incubation among crocodylians is accomplished entirely by decomposition of vegetation and solar energy with the only previously noted exception being *Paleosuchus trigonatus* which constructs nests either over or beside a termite mound which serves as the primary source of heat, an adaptation apparently associated with low ambient temperatures. With the sole exception of the mound-building megapodes, all extant birds use direct body heat to incubate their eggs. This is achieved by the hormonally controlled, seasonal appearance of a bald region on the parent's chest or belly, known as a brood patch that ensures that the eggs are in direct contact with the adult and not insulated from body heat by any feathers (e.g. Carpenter 1999; Elphick et al. 2003). The use of an incubating vegetation cover among dinosaurs has long been suggested, though as such material decomposes and is not normally preserved; this has proven difficult to demonstrate. One possible clue is gas conductance which is the rate of gas exchange that occurs through the pores of an egg with oxygen and carbon dioxide diffusing in and out, respectively. An egg buried in a humid mound with no source of oxygen will demonstrate a high gas conductance rate, whereas an egg in a dry environment where the risk of dehydration is high will in contrast have a low rate (e.g. Carpenter 1999). This theory was put to test by Seymour (1979) who examined measurements of both shell and pore geometry from *P. andrewsi*, *Hypselosaurus priscus* and a Gobi sauropod. Compared to extant avian and reptile nests with known nest environments, the three study species displayed high gas conductance values, each having highly porous eggshells that indicate a nest high in both humidity and carbon dioxide while low in available oxygen. This suggests either burial or decomposition via a mound of vegetation as the most likely incubation methods. It is interesting to note Seymour's (1979) observation that in order to prevent depletion of oxygen and the subsequent elevation of carbon dioxide to critical levels in the nest, sauropods may have had to either reduce the clutch size or split them into separate nests. This may cast light on the above-noted report of Moratalla and Powell (1994) who described sauropod clutches as containing small numbers of eggs often spread over a specified area or clustered pattern.

There have been several finds of adult coelurosaurian theropods associated with eggs, the first being the holotype of *Oviraptor philoceratops* from Bayn Dzak, Mongolia, which was described by Osborn (1924) as preserved while preying on a nest of *Protoceratops* eggs. It was later demonstrated by Norell et al. (1994) that the eggs were oviraptorid and that the holotype was not preying upon the

clutch but likely exhibiting pre-hatching parental care. Perhaps the most publicised find of this nature was the oviraptorid *Citipati* as reported by Norell et al. (1995) from Ukhaa Tolgod, Mongolia. The adult was positioned on the nest over the eggs with both hindlimbs tightly folded with both lower legs and feet almost parallel to one another. The feet were located on top and adjacent to the eggs on the inner perimeter of the circle defined by the nest. With the ischia covering the eggs at the posterior side of the nest, the pubis lay at the centre while the gastralia just posterior to the shoulder girdle are in contact with the eggs. The front limbs were directed in a posterior manner so that both arms appeared to wrap around the nest and the claws on both hands faced inward. Under the adult, there were at least 15, and possibly as many as 22, paired eggs arranged in a circular pattern so that the broad end of each egg pointed towards the centre of the nest. In some places, the eggs occurred in two distinct levels.

The third discovery of an adult oviraptorid on a nest was reported by Dong and Currie (1996) from Bayan Mandahu in Inner Mongolia. The adult was described as sitting on its haunches on top of the nest with both hindlimbs folded underneath the body. The right foot was positioned in the centre of the nest where no eggs are present and, as with the previous specimen, the right arm was folded back so that the hand lay outside and around the semicircle of eggs. The belly was situated over the centre of the nest and the relative position of the vertebrae indicates that the adult's body stretched out beyond the circumference of the nest. Overall symmetry of both the skeletal remains and the nest would suggest that at the time of death the adult was likely squatting with both feet within the circle of eggs. However, the back of the right foot is at a higher elevation than the eggs which would indicate that the centre of the nest may have been filled with sand and not eggs. As with the previous specimen, the six eggs and fragments of several others were laid in a circle in distinct pairs; however, as only a single layer was present, it is plausible that the adult may have died at some point during the oviposition cycle. The authors noted that the open sandy centre and position of the hindfoot could be a clue as to how eggs were laid. It was speculated that female oviraptorids deposited eggs while standing in one spot and turning clockwise in a circle. In this scenario, the first layer of the circle would have a wide radius though the spiral would tighten as additional layers of eggs were added. The base of the nest appeared to be at ground level which would indicate that in life the nest would have taken the form of a raised mound. A fourth adult oviraptorid apparently positioned over a nest is the unprepared material MAE 95-97 from Ukhaa Tolgod, where a good portion of the skeleton appears to be overlying a nest (see photograph in Webster 1996).

Originally mistaken as that of the hypsilophodontid *Orodromeus makelai*, a well-preserved nest of the

coelurosaurian theropod *T. formosus* was discovered at the Two Medicine Formation in Montana. The nest was a bowl-shaped depression surrounded by a distinct rim with an internal area of approximately 1 m². At the centre of the nest lay a clutch of 24 tightly packed eggs that had been partially buried in the ground so that only their upper portions were exposed. This clutch layout, apparently unique to *Troodon*, resulted in a configuration which tends to obstruct the original paired pattern. Unlike the previous *Oviraptor* specimens, no adult remains were found to be associated with the eggs (Varricchio et al. 1999; Varricchio and Jackson 2004b). A possible example of a dromaeosaurid associated with an egg was noted during an evaluation of materials from the Cloverly Formation in southern Montana. A series of rod-like bone fragments were found along with an abundance of eggshells. Originally identified as ornithischian ossified caudal tendons, the fragments were reinterpreted as the gastralia of *D. antirrhopus* (Makovicky and Grellet-Tinner 2000). As a portion of eggshell was discovered in partial contact with this articulated gastralia, it was suggested that there may have been a parental association between the two elements (Grellet-Tinner 2001) though considering the extent of taphonomic content lost during both excavation and preparation of the material (Grellet-Tinner and Makovicky 2006) some degree of scepticism would appear warranted. In contrast, Kundrat et al. (2007) noted that a therizinosauroid theropod clutch from China appeared to be part of a hidden subterranean nesting strategy with little to no pre-hatching attendance of the eggs.

The discovery of coelurosaurian theropods with feather impressions has led to speculation that this particular group of dinosaurs may have used a brood patch to incubate in a manner identical to extant avians, using direct physical contact with their eggs in an uncovered, open nest (e.g. see Norell et al. 1995; Dong and Currie 1996; Varricchio et al. 1999; Grellet-Tinner 2006; Grellet-Tinner et al. 2006). In regard to the alleged *Deinonychus* gastralia and eggshell association, Grellet-Tinner (2001) proposed that an avian methodology of egg brooding was an ancestral character for the Maniraptora and thus would be expected in the Dromaeosauridae. There is trace evidence that the phenomenon of monoautochronic ovulation, in which one egg at a time is produced per ovary at daily or greater intervals, occurred in at least coelurosaurian theropods (Sato et al. 2005). It has been suggested that a theropod-like *Troodon* would leave its eggs unincubated so that the ambient temperature would maintain embryonic development in stasis until completion of the clutch. At this stage, direct body contact between an adult and the eggs would raise the embryonic temperature above the ambient, initiate incubation and allow for synchronous hatching (e.g. Varricchio and Jackson 2004b). However, as not all extant birds exhibit synchronous hatching (Perrins 2003), it is unclear as to how

relevant this hypothesis is. In another similarity to extant avians, Norell et al. (1995) suggested that the eggs of oviraptorid nests were manipulated by the parent or parents into a specific configuration. However, the idea of egg rotation was questioned due to the undisturbed paired pattern of the eggs in favour of precise positioning by the female during oviposition (Dong and Currie 1996; Varricchio et al. 1997; Clark et al. 1999; Sato et al. 2005).

In a further nod to the idea of feathers being requisitioned towards a role in incubation of eggs, Hopp and Orsen (2004) proposed a hypothesis to account for the apparent lengthening process of the feathers on the forelimbs and tail of coelurosaurian theropods. These feathers could be spread to shield not only the eggs from both the elements and solar overheating while the parents incubated the eggs, but could also provide cover for the hatchlings (see also Hecht 1998). The idea of feathers acting as a shading mechanism was also proposed by Norell et al. (1995) for nesting oviraptorids. One problem with this hypothesis is that in consideration to the current fossil evidence, it is not easy to evaluate. While both true feathers and assorted types of integument have been reliably documented in numerous small sized coelurosaurians, such structures remain elusive for larger animals with only a series of long quill-like fibres described for the mid-sized 2.2 m long therizinosauroid theropod *B. inexpectus* (Xu et al. 1999a). A recent example of this complexity was the controversy surrounding the small dinosaur *Juravenator starki*, which was assigned to the Compsognathidae (Göhlich and Chiappe 2006). Other members of this family include *Sinosauropteryx* for which filament-like structures are well known; however, *Juravenator* was found with a patch of skin on the tail which is scaled with no sign of feathers, not even impressions of follicles that might indicate the loss of the same (Göhlich and Chiappe 2006; Xu 2006). A subsequent investigation by Butler and Upchurch (2007) verified the assignment of *Juravenator* as a compsognathid and noted that the Compsognathidae were basal to the Maniraptora. Integumentary structures are considered to be a synapomorphy of the latter clade (e.g. Martin 2005), so the problem remains of having one compsognathid with 'proto-feathers' and one with scales. However, this contradiction disappears should Lingham-Soliar et al. (2007) be correct with their controversial assertion that the filament morphology of *Sinosauropteryx* is a closer match to intradermal collagen fibres rather than epidermal follicular structures. The issue here is that there is no reliable way to predict the occurrence and distribution of such structures within theropods or, as has been demonstrated earlier, among other dinosaurian groups. It is plausible that the evolution of larger lineages of coelurosaurian theropods resulted in feathers being either lost or severely attenuated. Therefore, the hypothesis of whether taxa such as *Oviraptor* were equipped with an extensive cover of feathers and a brood

patch (or any other form of hairy covering) cannot be reliably tested at this time.

Many other investigators have noted problems concerning the concept of true avian brooding with the alternative hypothesis being that nests may have simply been guarded rather than brooded (e.g. see Hirsch and Zelenitsky 1997; Carpenter 1999; Ruben et al. 2003; Grellet-Tinner and Chiappe 2004; Deeming 2006). Several of the aforementioned oviraptorids associated with nests have been described as having certain skeletal elements such as the gastralia and ventral ribs resting directly on eggs which has been used as evidence for either brooding or use of a brood patch, though Clark et al. (1999) conceded that this may have been due to the action of gradually rotting vegetation bringing the eggs in closer contact to the body. As all of the nesting oviraptorids appear to have perished in rapid sand storms (e.g. Dashzeveg et al. 1995; Weishampel 1995b; Dong and Currie 1996), it is likely that the animal would have had little or no time to evacuate in favour of any possible refuge. Female crocodilians have been observed to lie directly across the top of their nests as a nest-guarding behaviour (Coombs 1989; Lang 1989). Deeming (2002, 2006) evaluated the available evidence and, based upon ultrastructural characteristics, water vapour conductance and eggshell thickness, concluded that the nests of *Oviraptor* and all other dinosaurs were fully buried and not brooded by an adult. The avian brooding hypothesis is further troubled by the observation that certain enantiornithine Mesozoic birds apparently buried their eggs in substrate, with no means of direct contact incubation (Deeming 2006). As these taxa were phylogenetically closer to neognatha than coelurosaurian theropods, parsimony would further suggest that the eggs of the latter were buried for incubation.

The hypothesis that *Troodon* eggs were partially buried with the exposed surfaces subject to incubation via direct physical contact (e.g. Varricchio et al. 1997; Varricchio and Jackson 2004b) deserves further evaluation. However, no trace evidence has been found to indicate or suggest the presence of an adult at any time during the nest's incubation and subsequent hatching. It is equally likely that as the eggs were laid in pairs, partial burial helped keep them in place to avoid damage with the exposed area allowing for the ambient temperature to initiate embryonic developmental stasis. Once the clutch was complete, the nest could have been filled with vegetation to activate incubation while perhaps being kept under guard by an adult. In conclusion, some manner of nest attendance is common in almost all extant archosaurs and a similar scenario would certainly appear to be the case for extinct members of this group. To date pre-hatching parental care has only been conclusively demonstrated in oviraptorids and with that in mind it can now be evaluated as to whether any post-hatching care may have occurred.

This paper has demonstrated that among the extant archosaurs, some mode of post-hatching parental care appears to be ubiquitous with the sole exception of the megapodes and avian brood parasites. All crocodilians that have been subject to long-term study show extensive female (and on occasion male) post-hatching care, which includes breaking open the nest to free hatchlings, their subsequent transport to a crèche and a period of active defence against predators or hostile conspecifics. Juvenile alligators may continue to maintain a parental association with their mother for up to 3 years (Coombs 1989). For birds, post-hatching care involves a variety of tasks including the feeding of hatchlings, cleaning of the nest and the protection of nest-bound hatchlings from predators (Elphick et al. 2003). While much neognath post-hatching care is provided by two parents, the paleognatha display a strong bias towards male care of not only eggs but also the resulting young (Hanford and Mares 1985). Most parental care observed in other reptiles such as squamates tends to involve pre-hatching egg tending and defence (e.g. see Shine 1988), though there are notable exceptions. As an example, the crocodile skink (*Tribolonotus gracilis*) engages not only in egg tending and nest protection, but also in sophisticated offspring defence tactics which involve vocalisations, social associations between females and their hatchlings and the maintenance of a close proximity of females and neonates for some duration after hatching (Hartdegen et al. 2001). It is clear that post-hatching care is well distributed among not only extant reptiles but also vertebrates and invertebrates in general and in that regard one can enquire as to what lines of evidence there might be for similar or equivalent behaviours in dinosaurs. Before continuing, it is wise to heed the warning of Coombs (1982) who cautioned that the morphological diversity and long evolutionary history of dinosaurs make it highly unlikely that every species practised a similar amount of parental care. Furthermore, the choice of extant analogue can result in a subtle trap that encourages interpretations far beyond what can reasonably be concluded from the actual data.

Among species, both the rate and stage of development varies considerably at parturition, and in that respect the young of extant archosaurs are often divided into the categories of either precocial or altricial based upon the level of required post-hatching care. The majority of vertebrates and invertebrates produce precocial young that have the ability to move, feed and even react to danger with little or no parental input stimulus. In contrast, altricial offspring are completely helpless if left alone and thus require a duration of parental help before they are capable of independence (e.g. Grier and Burk 1992). Hatchlings of crocodilians, paleognaths, galliformes, shorebirds and most waterfowl are precocial, so a single parent can often provide association for them alone, whereas most passerines and many other neognath

neonates are altricial to the point that they cannot maintain their own body temperature, and thus there is an extended period of biparental care (e.g. Böhme and Nickel 2000; Elphick et al. 2003; Fernandez and Reboreda 2003). However, the concept of precocial and altricial is simply two polar extremes, with many species producing young that do not fit neatly into either end of this altricial–precocial spectrum (Starck and Ricklefs 1998). On a related note, it is not possible to grade avian hatchling development on the altricial–precocial spectrum based upon either the degree or pattern of ossification of their skeletons (Starck 1996), nor can any general prediction be made regarding correlation between egg size and extent of parental care (Nussbaum and Schultz 1989).

There have been numerous descriptions of juvenile assemblages which may indicate that at least some dinosaurs formed exclusively all-juvenile groups. Currie (1989) reported an assemblage of five young ankylosaurid *Pinacosaurus* which appeared to have perished during a sandstorm, though no trace of any adult was found. Weishampel et al. (2000) reported 15 *Protoceratops* hatchlings that were rapidly buried in what appeared to be a bowl-shaped depression, suggesting that the scenario represented nest residents and evidence of an altricial mode of post-hatching parental care. However, no remains or trace elements of an adult were found associated with the alleged nest which may have simply been a natural depression in which a group of juveniles sought shelter before their subsequent demise and burial. Skeletal accumulations demonstrating age segregation of juvenile sauropods were described from both the Javelina Formation in Texas and the Morrison Formation in Montana (Myers and Fiorillo 2009). Apparent juvenile groups of the stegosaur *Stegosaurus* from the Morrison Formation in Utah and *Kentrosaurus* from East Africa were described by Galton (1982b). Juvenile aggregations of *Tenontosaurus* from Big Horn County in Montana led Forster (1990) to suggest that such post-hatching congregations were more widespread among ornithomimids than previously thought. A possible adult presence might indicate that these groups were tended, though whether or not these examples represent unequivocal evidence of adult-free associations remains ambiguous (Varricchio 2000). Regardless, such groupings of juveniles are not unusual and have been well documented in neonate green iguanas that often congregate with no form of parental supervision. Both hatchling and juvenile iguanas are highly social and demonstrate a variety of sophisticated social behaviours (e.g. see Burghardt 1977; Burghardt et al. 1977; Werner et al. 1987; Mora 1991). Moreover, these associations can act to heighten the chances of survival by allowing for increased vigilance and the dilution effect of large groups. Among extant archosaurs hatchling, crocodilians are known to remain in associations both during and after adult supervision (e.g. Coombs 1989).

Juvenile group formation has been suggested for *Psittacosaurus mongoliensis* associations from the Oshih Formation in Mongolia. The lack of any trace of an adult appears to suggest that these groups were precocial and self-feeding (Coombs 1980, 1982), though recent discoveries indicate that the situation may be more complicated. Meng et al. (2004) reported 34 fully articulated *Psittacosaurus* juveniles in close association with an adult, all of which had been rapidly entombed alive by volcanic fallout. Considering the physical size of an adult *Psittacosaurus*, it is highly unlikely that a female could produce a clutch of such size so the association may have represented a group of juveniles under the supervision of an adult, unless the adult presence was a chance event at the time of preservation. In the Yixian Formation in China, a group of six young *Psittacosaurus* were found which had been preserved during a catastrophic event (Qi et al. 2007). Age profiles of the herd members strongly indicate the presence of juveniles from at least two clutches, which, if correct, seems to support the aforementioned association of 34 juveniles being an association of several clutches.

The *Maiaasaura* nest trace from the Two Medicine Formation in Montana is arguably the best known of all egg, nest and hatchling material and is a common reference for post-hatching care. Horner and Makela (1979) chronicled a concave structure in which were found the remains of 15 *Maiaasaura* juveniles, each about 1 m in length. Remains of broken eggshell among the skeletons and evidence of extensive tooth wear were purported to represent the first substantive evidence of post-hatching parental care in dinosaurs, with the helpless nest-bound hadrosaurs being provisioned and tended by a parent or parents. A layer of vegetation was believed to have been used for incubation of the original circular clutch of eggs (Horner 1984; Horner et al. 2001). Further evidence of altricity was offered in the form of osteological work that suggested the femoral condyles of the *Maiaasaura* embryos were only partially formed, with the ends of the bones apparently spongy and incomplete (Horner and Weishampel 1988). Moreover, Horner (2000) reported that the limbs of the young hadrosaurs had calcified cartilage structures that would have limited locomotion to a great degree during the time between hatching and when the neonate doubled in size, so once more a semi-altricial developmental mode was proposed. The interpretation of a nest structure along with associated colonial nesting has already been evaluated and it remains unclear as to whether the structure described as a nest was being used as a familiar refuge by an all-juvenile group. Ground teeth were offered as proof that the neonates were being provisioned, but later discoveries of *Hypacrosaurus* from the Two Medicine Formation in southern Alberta indicate that in ovo embryonic hadrosaurs ground their teeth (Horner and Currie 1994; Lessem 1996; Carpenter 1999).

Geist and Jones (1995) noted that the long bone epiphyseal structures of neonate dinosaurs were being offered as evidence of altricity, though they cautioned that such descriptions closely resemble fossilised epiphyseal structures which may have been a result of losing the articular fibrocartilaginous cap prior to preservation. It was thus argued that that particular line of investigation left the altricial versus precocial development controversy unresolved. Geist and Jones (1996) thus evaluated the skeletal structures of extant perinatal altricial avians, precocial avians and precocial crocodilians with their skeletal features then compared these to those known for perinatal dinosaurs. During skeletal ontogeny in extant archosaurs, the morphology of the perinatal pelvic girdle appeared to be the most reliable indicator of developmental maturity. A well-ossified pelvis indicated a precocial developmental range, whereas a poorly ossified pelvis was more typical of the altricial range. As all known dinosaur hatchling specimens demonstrated the former level of ossification, it was thus concluded that *Maiasaura* and other fossil neonates were mobile and not nest bound.

Trackways from South Korea have yielded traces of dog-sized and therefore likely rather young sauropods milling around near their probable place of hatching, evidently not travelling in a set direction as revealed by the tracks of sub-adults and adults (Lockley 1990; see also Horner 1992). This segregation of young from the adult population has been noted during trackway and bonebed evaluations with the most probable reason being that only larger sub-adults could maintain the locomotive pace of the adult migrators (Carpenter 1999). The extensive nest traces of Auca Mahuevo in Argentina have yielded the remains of sauropod embryos including their skin imprints (Chiappe et al. 1998, 1999), though there did not appear to be any traces of adult supervision or post-hatching interactions with neonates. An apparent absence of any skeletal neonate or juvenile remains at nest sites tend to indicate precocial young (Moratalla and Powell 1994), although both *Apatosaurus* and *Camarasaurus* adults have been found in an apparent association with several juveniles that measured less than one quarter the adult size (Carpenter 1999). An embryo of the prosauropod *Massospondylus carinatus* from the Elliot Formation in South Africa was described as having a large head and forelimbs with a horizontally held neck. These characteristics would indicate that the embryo was an obligate quadruped, though in contrast the adults were capable of at least facultatively bipedal locomotion. The embryo appeared to lack well-developed teeth, all of which led to the suggestion that the hatchling would have been altricial and required extensive post-hatching care (Reisz et al. 2005; Stokstad 2005). One possibility not developed was that the differences between hatchling and adult morphology would have allowed resource partitioning to occur, a strategy that would have allowed the two

generations to exploit different food resources and in the process avoid direct competition with each other.

This fascinating ecological phenomenon has been very well documented among theropod dinosaurs. Both *Nanotyrannus lancensis* and *Stygimolator* were considered individual species until careful re-evaluation indicated that the taxa were in fact juvenile *T. rex* specimens. In the case of the former, the cortical surface of the bone displayed an immature grain so the fossil was clearly not that of an adult. In a similar sequence of events, it was shown that *Maleevosaurus novojilovi* was a juvenile *Tarbosaurus*. Moreover, it appears that a lengthened snout and the presence of non-serrated tooth patterns were generally typical characters of juvenile coelurosaurians (e.g. Carr 1999; Varricchio et al. 2002; Carr and Williamson 2004; Currie et al. 2005b). Similar differences in tooth morphology between hatchling and adult were reported for *Velociraptor* and *Troodon* (Carpenter 1999). A further examination of the skeletal structure in an embryonic *Troodon* revealed long distal segments and hindlimb proportions that were radically different from those of the adult form (Varricchio et al. 2002). While evaluating the maxilla of a hatchling *Allosaurus*, Rauhut and Fechner (2005) reported a shorter snout, fewer tooth placements and an unusually high degree of pneumatization in the skull when compared to adults. This raises questions concerning probable age structure components to any intraspecific resource partitioning that occurred in extinct archosaurs. Many extant species go through distinct age classes during their growth and as such the variety and type of food resource exploited by these differing classes can act to expand their niche width (e.g. Polis 1984). Furthermore, to date all theropod embryonic material indicates that the resulting hatchlings were highly precocial which has clear implications for hypotheses concerning the presence and level of post-hatching care. Norell et al. (2001) noted that in an embryonic oviraptorid from Mongolia, the overall degree of skeletal ossification suggested that the species was closer to the precocial end of the developmental spectrum. An evaluation of the skeletal remains of an embryonic *T. formosus* found cancellous tissue within the developing limbs that indicates a precocial condition for the resulting hatchlings (see also Horner et al. 2001). A well-preserved in ovo therizinosaurid embryo from China was reported by Kundrat et al. (2007) to demonstrate a level of skeletal development that strongly signalled highly precocial offspring.

It is entirely plausible that the overall precocial to superprecocial nature of described dinosaur hatchlings meant that post-hatching attendance was of rather little importance, as offspring would immediately disperse to exploit an ecological niche very different from that of their parents. It can be further conjectured that this lack of post-hatching parental care may have allowed many dinosaurs

to direct more of their energy into egg production, related reproductive effort and even physical growth instead of expending energy on actively defending and provisioning offspring. This phenomenon is by no means unique to dinosaurs and has been well documented in Mesozoic birds. An evaluation of late term enantiornithine *Gobipteryx minuta* embryos from the Lower Cretaceous of Liaoning, China, revealed imprints of wing and tail feather sheets. The presence of pennaceous wing feathers indicates that fledging occurred early during ontogeny and adds strong support for precocial young in this group (e.g. Elzanowski 1981; Zhou and Zhang 2004; Chiappe et al. 2007). Another enantiornithine specimen from the Rio Colorado Formation in Argentina boasts skeletal characteristics that indicate superprecocial flight capability (Elzanowski 1995). Such precocial offspring in the Enantiornithes, a group with a much closer phylogenetic relationship to Neoaves than coelurosaurians, adds further weight to precocial neonates in dinosaurs.

The evolutionary basis of the precocial–altricial developmental spectrum in birds was evaluated by Dial (2003) who proposed a unique model based upon both life history and mode of locomotion that incorporated flight capacity, nesting biology, body mass, stage at hatching and morphological modularity. When a specific taxon is assigned a place within a graph that considers these five character states, an interesting trend develops. On one polar end are basal extant species (e.g. megapodes, ratites, most Galliformes and some Anseriformes) which demonstrate the character states of a relatively large body size, superprecocial to precocial offspring, locomotion dominated by the hindlimb, minimal levels of parental care, flightlessness or brief bursts of flight and simple ground nests. On the other extreme end of the spectrum are the derived extant Passeriformes which represent the character states of a small body size, altricial to superaltricial offspring, pronounced forelimb investment, intensive levels of parental care, full flight capability and broad nesting habits (see Figure 15 for the placement of various avian families in the above continuum). It is interesting to note that the characters for basal birds would seem to be fairly consistent with the albeit limited data previously described for theropod dinosaurs which had a large body size, highly precocial offspring, a mode of locomotion that was clearly dominated by the hindlimb, minimal to no parental care, flightlessness and constructed simple ground nests. In summary, all advanced parental care in extant birds is strongly correlated with a shift from the hindlimb to the forelimb as the primary means of locomotion as the resulting nest-bound young require extensive shelter and provisioning (after Dial 2003).

Bakker (1997) reported evidence of *Allosaurus* ‘lair’s from the Morrison formation in the western United States. Tooth marks apparently made by both small and large *Allosaurus* were found on large sauropod bones which led

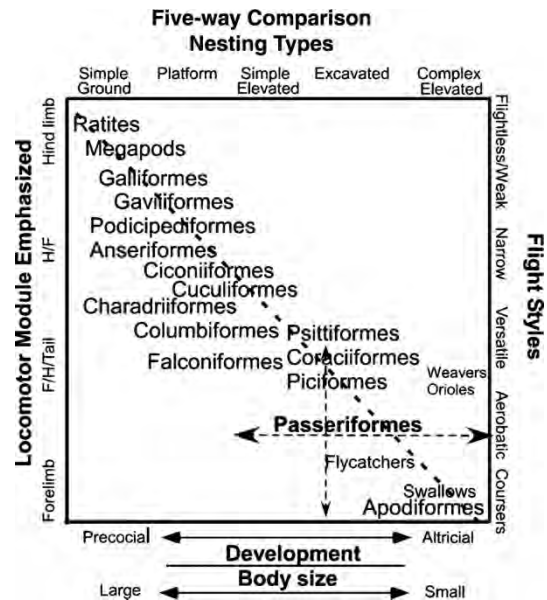


Figure 15. Placement of major avian families in the post-hatching parental care continuum. From Dial (2003); figure courtesy of the The Auk and the American Ornithologists' Union.

Bakker to suggest that adults dragged carcass fragments to their concealed young and that offspring remained with their parents until fully grown. In contrast to this interpretation, it is more likely that the ‘lair’ sites are the remains of cannibalised *Allosaurus* surrounded by the shed teeth of conspecifics, a situation that would imply a hierarchical feeding structure in which larger animals fed first (Bakker and Bir 2004; Roach and Brinkman 2007). The first evidence for true fossorial behaviour among dinosaurs was found at the Blackleaf Formation in southwest Montana. An adult and two juveniles of the hypsilophodontid *Oryctodromeus cubicularis* were discovered in the expanded distal chamber of a sediment filled burrow, with the correspondence between the dimensions of the adult and the burrow strongly suggesting that the animal was responsible for creating the tunnel. Further evaluation of the skeleton yielded several features consistent with digging behaviour though the hindlimb proportions remained cursorial. It was proposed that fossorial habits may have been an adaptation for predator avoidance, the rearing of young or the exploitation of a harsh environment (Varricchio et al. 2007). Regardless of such interpretations, this unequivocal association of an adult and two juveniles can be considered the first truly definitive evidence of post-hatching parental care in dinosaurs.

It has become clear that there are several key reproductive features that are shared by both extinct and extant archosaurs. Extant birds and crocodilians all produce hard shelled eggs, exhibit both pre- and post-hatching care, have a similar luteal morphology and

oviposit using an assembly line mode of egg production. However, crocodilians deposit a large number of small sized eggs that are ovulated, shelled and laid all at once to be incubated in vegetation or sediments. In contrast, neornithines produce far fewer but larger sized eggs which are ovulated, shelled and laid one at a time in open nests to be incubated via direct body heat. Coelurosaurian theropods share the ancestral characters of two functional oviducts and a lack of egg rotation though exhibit derived avian traits that include the production of one egg per oviduct and maintaining an initial open nest to encourage embryonic stasis via an ambient temperature regime until the clutch is complete. In terms of post-hatching care, it appears that coelosaurian theropods all retained self-feeding and highly precocial young, an ancestral character common to crocodilians and the basal avian Paleognathae, Galliformes and Anseriformes. It seems evident that nest-bound, superaltricial offspring requiring a high degree of biparental attendance is a derived feature that occurs within the neognatha above the Galliformes and Anseriformes (Varricchio et al. 1997, 1999, 2002; Varricchio and Jackson 2004b; Sato et al. 2005). Controversies surrounding the evolution of extant avian care systems will be outlined and discussed in the next section.

3. Discussion

The inherent difficulty in extrapolating dinosaur behaviour based upon fossil evidence has been noted previously (e.g. Witmer 1995). It has been demonstrated that although much that can be gleaned from the fossil record is of limited utility, a few promising avenues persist. These include hypotheses concerning the putative roles of cranial ornamentation, the possible herding activities of many herbivorous dinosaurs based upon trackways and mass accumulations, and the similarities of certain reproductive apparatus in extinct coelurosaurian theropods and extant Aves. In the latter respect many investigators have attempted to demonstrate that avian reproduction boasts an explicit theropod evolutionary origin in terms of gonadal structure and function, physiology, incubation strategy and post-hatching parental care behaviour (e.g. see Larson 1998; Prum 2002; Varricchio and Jackson 2004b; Grellet-Tinner 2006; Grellet-Tinner et al. 2006; Zelenitsky 2006; Varricchio et al. 2008a).

There is no universally accepted definition of 'parental care' though there exist two distinct variants, those being pre- and post-parturition. Both are widespread throughout vertebrate and invertebrate taxa (e.g. see Alcock 1989; Grier and Burk 1992). Extensive levels of both types provided biparentally are a phenomenon almost exclusive to birds, as by comparison most other taxa demonstrate either uniparental or female-only attendance (e.g. Clutton-Brock 1991). Here the term 'parental care' is defined as any behaviour undertaken by a parent or parents who act

to defend or provision neonates unless otherwise noted. Currently, there are three distinct and competing theories concerning the evolution of extant avian parental care which describe the ancestral condition as being biparental (e.g. Lack 1968; Emlen and Oring 1977; Kavanau 1987, 2007; McKittrick 1992; Krebs and Davies 1993), paternal (e.g. Van Rhijn 1984; Elzanowski 1985; Van Rhijn 1990; Wesolowski 1994; Ligon 1999; Vehrencamp 2000; Wesolowski 2004) or maternal (e.g. Burley and Johnson 2002; Tullberg et al. 2002). This section investigates these hypotheses and evaluates what relevance each has in consideration to ichnological evidence. Firstly, though, it is important to summarise the ideas regarding the evolution of extant avian parental care.

3.1 Hypothesis one: biparental care as ancestral

Because biparental care occurs in approximately 90% of extant birds, the classical view has long considered that the first birds exhibited advanced biparental care with effort focused on how deviations from this ancestral state might have been achieved (e.g. Wesolowski 1994). The most detailed model of this hypothesis was by Kavanau (1987, 2007) who proposed the occurrence of six distinct stages from reptilian ancestors to ancestral birds. In stage one, a scaled ectothermic hypothetical ancestor buried multiple eggs and employed solar radiation for incubation. At this point, both of the ancestral female's ovaries are fully functional with ovulation polyautochronic and any care is limited to egg guarding. In stage two, a partially arboreal lifestyle is achieved and the scales now have a feather-like appearance, though physiology remains unchanged. Adults attend multiple clutches which are incubated by solar radiation and/or by physically shading or exposing the eggs. A primitive variation of endothermy and feathers optimised for parachuting from height usher in stage three, along with polyallochronic ovulation in which multiple clutches are formed in rapid succession by alternating between ovaries. Both sexes brood the eggs using direct contact and exhibit some degree of post-hatching defence of the young. At stage four, full flight capability is achieved with a single egg being produced by one alternating ovary or monoallochronic ovulation. It is suggested that at this stage nest-bound and altricial young would have appeared and thus a higher degree of post-hatching care by both parents. Both fully feathered and endothermic, the stage five ancestral bird has both sexes maintaining one clutch produced by a single functional ovary. Modern birds are represented by stage six which is hallmarked by strong trends to both arboreal nesting and superaltricial offspring. McKittrick (1992) constructed a phylogenetic analysis of 60 extant avian taxa using both parental care behaviour (15 characters) in tandem with anatomical data (69 characters), which inferred biparental care as ancestral for birds and that biparental incubation

has its origins in an ancestral condition in which neither sex incubated. In a more recent analysis, Tullberg et al. (2002) attempted to reconstruct ancestral parental care systems in a phylogeny that included all the primary extant amniote lineages. Transitions between the character states of no parental care, female-only care, biparental care and male-only care were inferred using two distinct resolutions for the most basal avian branches of the phylogenetic tree. Female-only care was inferred for the lineage leading to extant archosaurs, whereas a phylogeny in which (1) the paleognatha act as a sister group to the neognatha and (2) an ordered character-state assumption is employed, resulted in biparental care as the ancestral condition for neognatha.

3.2 *Hypothesis two: paternal care as ancestral*

An ancestral state of paternal care was proposed by Wesolowski (1994, 2004) based upon an amalgamation of 'cost-benefit' economic modelling and an historic overview of parental care systems. This hypothesis suggests a series of transitional states within the avian lineage beginning with no care to male-only to biparental. The theory is intimately associated with both powered flight and an initial increase followed by a decrease in overall egg size. The first step begins with an ancestral bird exhibiting no parental care and in that respect, larger eggs would be selected to allow for highly precocious neonates to fly soon after hatching. Such large eggs required a considerable investment of energy by females and in response the next stage envisions sequential ovulation with the male combining the attraction of multiple mates via territoriality and caring for the ensuing clutch. This scenario would allow females, no longer constrained by the cost of sustained nest attendance, to dramatically increase their fecundity. Up to this point male care involved egg guarding, though the appearance of incubation via direct contact brooding by the male led to an increased need for parental attendance. Synchronous hatching paved the way for post-hatching care and once this occurred, egg size could diminish and thus allow for more altricial development. Once parental care became obligatory and conditions demanded the constant presence of a parent, the only way this could be achieved was by a pair taking turns attending the nest. This final stage yielded biparental care with both sexes assuming identical roles and could be further modified with gender role specialisation, uniparental double clutching or by reducing the role of one gender to either female-only care or ancestral male-only care. Similar models of unaided male care derived from a hypothetical reptilian ancestor exhibiting no parental care have been suggested by other investigators (e.g. Van Rhijn 1984, 1990; Hanford and Mares 1985). Ligon (1993, 1999) further argued that the initial method of parental care in birds began as simple egg

guarding from predators. The cost of nest defence can be expected to be high for females in terms of production of eggs. In contrast, such behaviour is less of an issue for males. Therefore, it can be hypothesised that females should refrain from parental care after oviposition, leaving both pre- and post-hatching responsibility to the attendance of a male.

3.3 *Hypothesis three: maternal care as ancestral*

A unique theoretical model independent of any specific phylogeny and with female-only care as the ancestral condition for birds was proposed by Burley and Johnson (2002). The hypothesis traces both key behavioural tactics and life-history characters that are associated with the transition from a 'reptilian' promiscuous mating system with no form of parental attendance to the social monogamy and biparental care that typifies many extant birds. The model has four distinct transitional phases. At stage one, female basal archosaurs were promiscuous, buried their eggs in substrate, incubated via solar radiation and were limited to maternal nest guarding. Innovations at this stage that increased the probability of neonate survival included (a) an increase in egg size and/or a decrease in clutch size; (b) surface nesting with sequential rather than en masse oviposition with direct contact brooding and (c) an increase in mate choice by females and strong female-biased dispersal from natal territory. Further changes include increased maternal investment in precocial offspring and population sex ratios becoming male biased. Stage two is marked by pre- and post-courtship consortships between sexual partners that allowed males to both assess paternity and provide male care while providing females with the ability to evaluate mate quality. By stage three, the relative scarcity of females meant that females were able to select for increased paternal investment, a result of which is an escalation in mate choice for both sexes. This gradual growth in parental investment initiates stage four and the appearance of altricial neonates co-evolving with elevated biparental care, a result of which is social monogamy. It should be noted that this model suggests stage three as the most likely appearance of male-only care should selection pressures favour more precocial offspring.

3.4 *Relevance to dinosaurs*

The biparental theory of Kavanau (1987, 2007) depends heavily upon the presence of flight, endothermy for incubation and multiple modes of ovulation. Feathers and filamentous integument are well documented in coelurosaurian theropods which appear to agree with the aforementioned stages two and three. However, it remains unclear as to that both the extent of an arboreal mode of life

in these taxa and the unpredictable distribution of integumentary structures among the Dinosauria add a further confound. The hypothesis further predicts that nests become open to the elements and as a result brooding occurs by direct physical contact, the latter of which requires an endothermic physiology. It has been shown that there is currently no reason to believe that coelurosaurian theropods constructed or maintained fully open nests nor incubated via body heat. Furthermore, current ideas concerning the nature of dinosaur physiology remain controversial and contradictory (e.g. see Spotila et al. 1991; Ruben et al. 1996; Reid 1997; Seebacher 2003; Chinsamy-Turan 2005; Gillooly et al. 2006 and references within). Kavanau (1987) further suggests an alternating mode of ovary function which begins polyautochronic (multiple eggs from two ovaries) to polyallochronic (single eggs alternating between each ovary) to mono-chronic (a single egg from one functional ovary). Fossil trace evidence suggests that coelurosaurian theropods were monoallochronic, producing one egg from each of two functional ovaries (e.g. see Sato et al. 2005). In contrast, non-coelurosauians, such as the tetanuran theropod *Lourinhanosaurus antunesi*, appear polyauto-chronic based on analysis of nest contents (e.g. Mateus 1998). The biparental theory relies on hatchlings that are nest bound and altricial though all known fossil theropod hatchlings appear to have been precocious. In summary, the biparental model has limited support in terms of predicted integumentary structures, but in all other respects it does not conform with the current trace evidence. Moreover, as much of this model relies upon behaviours that are unlikely to be preserved, the hypothesis cannot be subject to rigid evaluation.

The maternal ancestry of parental care hypothesis of Burley and Johnson (2002) is confounded by being based almost exclusively upon theoretical behavioural and mate choice models that are not ideally suited for fossil preservation. Nonetheless, coelurosaurian theropods exhibit an increase in overall egg size, apparently exhibited monoallochronic ovulation and appear to meet most of the basal requirements of stage one with the notable exception of contact brooding. Furthermore, there is no predicted decrease, but rather an increase in overall clutch size among theropods, and other dinosaur clades (e.g. hadrosaurs) demonstrate increased clutch size despite their distant phylogenetic relationship to birds (Varricchio and Jackson 2005). The theory further assumes that the paleognaths are ancestral to the neognaths whereas in regard to any such relationship the fossil record is very unclear (e.g. Wesolowski 2004). Despite these difficulties, detailed phylogenetic analyses suggest that the maternal ancestry hypothesis is a viable mode of investigation (Tullberg et al. 2002) which will be investigated in detail below.

The increasing size of eggs and mate choice theory are key aspects of the paternal care ancestry hypothesis.

Coelurosaurian theropods appear to demonstrate an increase in the relative size of both eggs and clutches with trace fossil evidence strongly supporting precocial offspring. It is postulated that large eggs would produce precocial offspring able to quickly evacuate the nest, which in turn drove sequential ovulation. This allows a female to maximise her reproductive effort by depositing eggs in several nests attended by a male (Wesolowski 1994). However, it has been shown that there is no correlation between the size of an avian egg and the amount of parental care provided (Nussbaum and Schultz 1989), an observation that hampers the overall utility of this theory. There is a further prediction of sequential oviposition and contact brooding, the former of which has been strongly suggested in coelurosaurian theropods only (e.g. Sato et al. 2005), while the latter remains highly unlikely (Deeming 2002). The theory can be further influenced by the possible role of the Enantiornithines and other Mesozoic birds. If powered flight were to appear in the first stage, the model would predict the evolution of extant avian reproduction occurring mostly within the basal birds. However, should Enantiornithines, based upon their unique histology and growth, represent a divergence, then the origin of avian reproduction may be found within more basal regions of the coelurosaurian theropod clade (see Varricchio and Jackson 2005). It has been argued that should the latter prove correct, then the model could be used to predict that adult theropod fossils associated with clutches were male. Expanding on this theme, it is further suggested that as coelurosaurian clutches tended to be larger than predicted values, this may be an indication of communal nests used by multiple females (Varricchio and Jackson 2005).

The idea of paternal care in extant birds having such a dinosaurian origin was examined in greater detail by Varricchio et al. (2008a) with a hypothesis based on two distinct lines of evidence: clutch volume and bone histology. Among many extant birds, paternal-only and biparental care appear to correspond with the largest and smallest clutch volumes, respectively. Evaluation of four archosaur parental care type regressions reveal that the large clutch volume of oviraptorids and *Troodon* scaled most closely to the paternal mode of care in extant avians. Furthermore, an analysis of the long bones of the 'brooding' oviraptorids associated with nests revealed an apparent lack of medullary bone tissue which was interpreted as concluding evidence that the specimens were undoubtedly male (Martill et al. 1996; Varricchio et al. 2008a). It was thus argued that a male-only parental care system evolved before the emergence of extant birds and thus represents the avian ancestral condition. However, the hypothesis is undermined by the claim that the apparent lack of medullary tissue signifies gender. There is of course the old adage that absence of evidence does not mean evidence of absence, but the problems are more substantive than rhetorical language can attest.

The positive identification of bone structures such as medullary tissue remains problematic (e.g. see Kaye et al. 2006, 2007, 2008; Kaye and Gaugler 2008) and although the tissue of extinct and extant taxa may appear to bear a strong visual homology, whether or not that homology extends to being functional is currently unknown and likely untestable (e.g. see Werning and Lee 2006). Future evaluations of the long bone histology for the Sato oviraptorid and a *S. prima* specimen, both of which were described with preserved internal paired eggs (Chen et al. 1998; Sato et al. 2005), could yield valuable insight in regard to this controversy. Furthermore, in extant birds, medullary tissue is resorbed during egg shell formation (Taylor 1969; Bannister and Candlish 1973). Therefore, a more parsimonious interpretation may be that oviraptorids associated with nests were females whose medullary tissue had been depleted at the completion of their clutch. Observations regarding clutch volume regressions may or may not be significant as an observed relationship between two variables is not necessarily causal, and in studies involving extinct taxa, it is difficult to identify potential lurking variables and influential outliers.

3.5 Character evaluation

The preceding hypotheses place much emphasis upon behavioural data such as male–female interactions, mating strategies and the role of mate choice, none of which is or can easily be documented from the fossil record. However, all three hypotheses incorporate in one manner or another reference to the presence of feathers or related proto-integument, structure and layout of nests, the size of both eggs and clutches, the precocial–altricial sliding scale of hatchling development and function of the oviducts. Previous investigations have proposed a wide range of extant archosaur traits that could potentially be used as analogues for dinosaur nesting strategies and parental behaviours (e.g. Coombs 1989; Varricchio and Jackson 2005), and attempts have been made to phylogenetically map these traits (e.g. Varricchio et al. 1999; Horner 2000; Varricchio 2000). Using both the aforementioned reviews and the author's own investigations, this study gathered 28 potential behavioural and anatomical characteristics that may shed light on the evolution of archosaur reproductive strategies. The utility of many of these putative characters has already been outlined and discussed in detail, though given the importance placed upon certain traits by the competing theories, a recap will be made before any attempt is undertaken to evaluate which hypothesis is most parsimonious.

Obligate oviparity

All extant archosaurs demonstrate obligate oviparity due to the physiological need for oviposition to occur at the

early stages of embryonic development (Packard et al. 1977; Andrews and Mathies 2000). Trace evidence of nests and eggs and extant phylogenetic bracketing suggests a similar mode of reproduction for Dinosauria.

Hard-shelled eggs

The eggs of all extant archosaurs have a thick, hard shell composed of calcite crystals covered with pores which allow for the diffusion of respiratory gases (Packard et al. 1977; Carpenter 1999).

Embryonic eggshell use

In all extant archosaurs, eggshell calcium is used during mineralisation of the embryonic skeleton (see Packard et al. 1977; Andrews and Mathies 2000) which effectively ties the Archosauria to hard-shelled ovipary.

Phallic structure

The males of all crocodilians, paleognaths and Anseriformes have a phallus, though that of the Galliformes is considered non-intromittent. The highly conservative design of the archosaur phallus is a pair of connected fibrous bodies with a medial seminal groove which everts via the infusion of either blood or lymphatic fluid (King 1981a). Extant phylogenetic bracketing and an overview of dinosaur anatomy strongly suggest the presence of a similar phallic structure in extinct archosaurs.

Polyautochronic ovulation

The condition of ovulating multiple eggs from two ovaries was apparently the ancestral state for Archosauria and is well documented in crocodilians and non-coelurosaurian theropod dinosaurs (e.g. Mateus 1998; Chiappe et al. 1999).

Assembly line oviduct morphology

The reproductive tract of extant female birds differs from other oviparous amniotes in that both eggshell membrane production and calcareous layer occur in separate regions of the oviduct. Similar specialised uterine regions have been described in the crocodilian oviduct and are considered to be homologous to the avian condition (Palmer and Guillelte 1992) which makes this 'assembly line' morphology unique to all extant archosaurs.

Female sperm storage

This phenomenon is widely distributed in crocodilians (e.g. Davenport 1995; Gist et al. 2008) and avians (e.g. Birkhead and Møller 1992b) and is well documented in other reptiles (e.g. Gist and Congdon 1998; Sever and Hamlett 2002). Clearly, it is not possible to test for this

character using fossil remains, though its presence in extant archosaurs and other 'reptilian' lineages would suggest this as a likely dinosaurian trait.

Temperature-based gender determination

The sex of a crocodilian embryo is determined by the temperature of the nest during incubation (e.g. Ferguson and Joanen 1982; Deeming 2004), whereas, in contrast, that of an extant avian is genetically fixed by heteromorphic sex chromosomes (e.g. Standora and Spotila 1985). It is not possible to test for such a trait using the fossil record, though parsimony might suggest that dinosaurian taxa employed the ancestral condition.

Nest construction

All extant archosaurs construct a nest in which to deposit their eggs and the type produced tends to be distinct to each extant group. Crocodilians construct nests by either excavating a hole or scraping a mound composed of vegetation and detritus (e.g. Greer 1970). Paleognatha deposit eggs in a simplified scrape whereas among neognatha there is a trend towards arboreal nest construction (e.g. Elphick et al. 2003; Perrins 2003). Fossil evidence shows that sauropods appeared to be hole nesters (e.g. Chiappe et al. 2004), hadrosaurs built mounds (e.g. Thulborn 1992), oviraptorids a simple scrape (e.g. Dong and Currie 1997; Clark et al. 1999) and *Troodon* a scrape lined with a distinct rim (e.g. Varricchio et al. 1999). Some workers have suggested that the scrape nests of coelurosaurians were open with the adult(s) brooding the clutch via direct contact (e.g. Norell et al. 1995; Varricchio et al. 1999), though re-evaluations of available data indicate that these nests were most likely covered post-oviposition (e.g. Carpenter 1999; Deeming 2002, 2006).

Pre-hatching parental care (nest guarding)

Parental guarding of nests and clutch attendance is widespread throughout both birds and crocodilians (e.g. Böhme and Nickel 2000; Elphick et al. 2003) and has been suggested for dinosaurs based on trace evidence and parsimony (e.g. Carpenter 1999; Ruben et al. 2003; Grellet-Tinner and Chiappe 2004).

Uniparental female care

Post-hatching parental attendance is near exclusive in crocodilians (e.g. Böhme and Nickel 2000) and is common among the Galliformes and Anseriformes, although in the latter two groups biparental care does occur in a number of taxa (e.g. Perrins 2003). However, whether this is an ancestral trait or a homoplasy remains unclear.

Precocial young

The neonates of crocodilians, paleognatha, galliformes and anseriformes are highly precocial, primarily self-feeding and as such there is a strong bias towards female post-hatching parental care (e.g. Böhme and Nickel 2000; Dial 2003). Evaluation of fossil trace evidence and phylogenetic modelling strongly suggests precocial offspring for all dinosaur taxa.

Integumentary structures

A range of simple filaments to modern feathers have been described for numerous small theropod taxa including compsognathids (Currie and Chen 2001; Ji et al. 2007), a tyrannosaurid (Xu et al. 2004), dromaeosaurids (Ji et al. 2001), an oviraptorid (Ji et al. 1998) and a troodontid (Xu and Norell 2006). Similar structures have been reported from the ceratopsid *Psittacosaurus* (Mayr et al. 2002) and the heterodontosaurid *Tianyulong* (Zheng et al. 2009), although it remains unclear as to whether these are homologous or a result of independent evolution. It has been suggested that in coelurosaurian theropods, these structures represent evidence of direct contact brooding and brood patches, though a critical evaluation reveals severe deficits with this idea with the more parsimonious role of display function being favoured (see discussion in previous section).

Monoautochronic ovulation

All extant female birds can only ovulate one egg at a time, whereas crocodilians ovulate the entire clutch (Jones et al. 1979; Lance 1989). Fossil nest and egg evidence clearly reveal that coelurosaurian theropods produced two eggs at a time in an unusual 'fusion' of both the ancestral crocodilian and the derived avian states (Sato et al. 2005). This mode of oviposition may have been influenced by body size, with small coelurosaurians unable to maintain large clutches internally. Considering the trend towards gigantism in this clade, it is unclear whether larger animals such as *Tyrannosaurus* would have produced two eggs at a time or simply ovulated the entire clutch. However, in stark contrast, all other dinosaur taxa appeared to have maintained the ancestral condition (e.g. see Mateus 1998; Chiappe et al. 1999).

Eggshell microstructure

Extant birds and coelurosaurian theropods share numerous egg and shell structural characteristics that are considered to be either shared or convergent to the point at which no single trait can be used to differentiate between the two taxa (e.g. Varricchio et al. 2002; Varricchio and Jackson 2004a).

Large egg size

Large sized eggs have been reported for several coelurosaurian theropods (e.g. Varricchio et al. 1997) and lambeosaurines (e.g. Horner 1999). In relation to body size, avian eggs tend to be noticeably larger than those of reptiles and while dinosaur eggs are smaller than those predicted for similar sized birds, they nonetheless remain larger than reptilian eggs (see Blueweiss et al. 1978). This phenomenon led Varricchio and Jackson (2003) to propose the distinct possibility of two independent enlargement trends in the Maniraptora and Hadrosauridae clades. However, as a caveat it must be noted that size can be difficult to establish in fossils, which leaves room for variable interpretations.

Clutch size

The weight of a clutch is noticeably larger in reptiles than in birds when adult weight exceeds nine kilograms (see Blueweiss et al. 1978). Among dinosaurs, Varricchio and Jackson (2003) compared data indicating clutch weights that were estimated to be smaller than average (e.g. titanosaurid), average (e.g. lambeosaurines) and larger than average (e.g. *Troodon*, *Oviraptor*). Underground nests apparently used by sauropods and hadrosaurs only allow for smaller clutches due to the limitations of embryonic gas exchange (Seymour 1979), whereas the unusually heavy clutches of theropods, up to four times that expected for both birds and reptiles, may represent either a communal effort (Varricchio and Jackson 2003) or some other unknown quantity not preserved in the fossil record.

Delayed incubation

Avian reproductive biology is unique in that a single egg at a time is laid, with the result that an entire clutch can take several days to be laid and to hatch. The ensuing eggs do not begin to develop until a particular temperature regime is reached during direct contact incubation (e.g. Elphick et al. 2003). This delay of embryonic development may have occurred in coelurosaurs [Sato et al. 2005; though see Wesolowski (2004) for a counterpoint] and should that be the case then perhaps nests were left open to ambient temperatures until the clutch was complete, at which point the eggs were buried under substrate to initiate incubation.

Loss of right ovary and oviduct function

All extant female birds with the sole exception of the Apterygidae have one functioning left oviduct whereas in contrast, female crocodilians have two fully operational ovaries (King 1981a). Fossil trace evidence has established that coelurosaurian theropods maintained the ancestral condition of producing eggs from paired ovaries (e.g. Chen et al. 1998; Sato et al. 2005).

Chalazae

This structure is composed of a spiral band of tissue that securely anchors the yolk in the centre of the albumen which allows the egg to be manually rotated by the parent without risk of damage to the embryo (Packard et al. 1977; Carpenter 1999).

Egg rotation

Fluid dynamic models strongly suggest that extant avian parents manually rotate their eggs to enable mixing in the albumen which acts to both provide the embryo with nutrients and disperse waste products during the early stages of incubation. Rotation is not required to allow for the uniform heating of eggs (Edwards et al. 2003). The structure and arrangement of dinosaur clutches and nest traces strongly indicate that rotation could not have occurred (Carpenter 1999).

Eggs uncovered and exposed

Crocodylians bury their eggs in either excavated holes or vegetation mounds (e.g. Greer 1970), whereas avian nests, with the exception of the megapodes, are open to the ambient environment and as such are free of sediment (Elphick et al. 2003). The previous section discussed whether dinosaur nests were covered or exposed and concluded that the former was most parsimonious given the available evidence.

Genetically fixed gender determination

The gender of extant avian hatchlings is determined by heteromorphic sex chromosomes, in direct contrast to that of crocodilians and chelonians (see above).

Incubation by brooding

While crocodilians use solar energy and decomposing vegetation mounds to incubate their clutches (Greer 1970), all birds with the sole exception of the megapodes use direct physical contact between the parent and clutch to generate heat (Elphick et al. 2003). It has been widely proposed that coelurosaurian theropods incubated their clutches using the avian direct-contact method (Varricchio and Jackson 2004b; Zelenitsky and Therrien 2008), though the various confounding variables that conspire to make such a scenario highly unlikely have already been reviewed.

Uniparental male care

This mode of post-hatching parental care is almost exclusive in paleognaths (e.g. Bruning 1974; Perrins 1990) with the exception of Struthioniformes in which there is assistance from a major hen (Bolwig 1973) and

in Apterygiformes where the single neonate survives on its internal yolk sac until it begins to self-feed (e.g. Davies and Jolly 2003). It is less common among neognatha in which there is a strong trend towards biparental care.

Loss of phallus

The intromittent organ has been lost in the neognatha which rely upon direct cloacal apposition for transfer of male gametes to the female oviduct (King 1981a).

Nest-bound altricial young

It has been demonstrated that in extant birds all advanced post-hatching parental care is strongly correlated with powered flight as a primary means of locomotion. In contrast, the characters described for basal avians are similar to those suggested for theropods and include simple ground nests, flightlessness and locomotion dominated by the hindlimb (see Dial 2003).

Biparental care

Male and female post-hatching parental attendance is the typical behavioural repertoire for neognatha with the notable exceptions being the mound-nesting Megapodiidae in which the young is left on its own and the nest parasites (e.g. European Cuckoo) which use other avian species to incubate and provision their eggs (e.g. Elphick et al. 2003; Perrins 2003). For the same reason as noted above, it is the standard mode of care in neognath taxa.

This combination of both behavioural and anatomical characteristics in a cladistic analysis is by no means unreasonable, as behavioural traits have been successfully incorporated into phylogenetic mapping in other studies. Paterson et al. (1995) tested whether behaviour could accurately reflect the evolutionary relationships among seabirds. It was demonstrated that foraging, agonistic and reproductive behaviours were congruent with a molecular tree and that behaviour can indeed contain phylogenetic information. Furthermore, Senter (2008) mapped stereotypic visual and acoustic signals onto a phylogeny of several crocodilian species. The results indicated that for Alligatoridae and Crocodylidae, late Cretaceous ancestral behaviours included circling, bubbling and geysering, mutual snout rubbing and rubbing the snout along the dorsal surface of an intended mate. It should nonetheless be noted that considering the highly plastic nature of behaviour, it is both reasonable and advisable to ensure that the behavioural traits chosen are kept as basal as possible to minimise the injection of confounds into any putative phylogenetic model. This is likely to be even more important when dealing with extinct clades for which data are either unavailable or open to interpretation. In that respect note that in the preceding list of characters no inclusion has been made of, for example, courtship

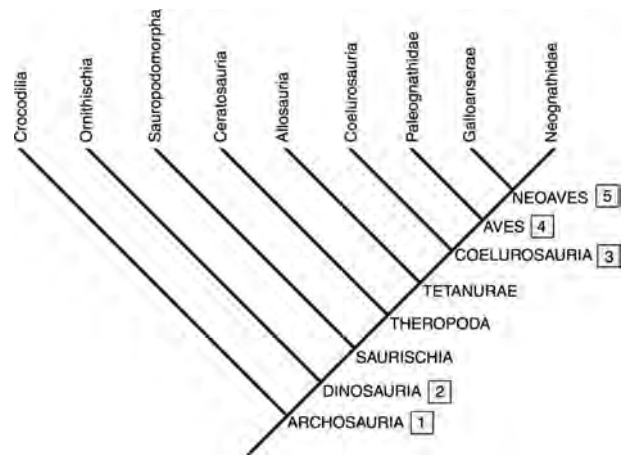


Figure 16. Cladogram outlining a phylogeny of the Archosauria with mapped reproductive features demonstrating a series of quantifiable evolutionary steps leading to the Neognathae. See text for a detailed listing of characters associated with each stage (cladogram after Varricchio et al. 1999).

routes or social organisation. It should be noted that there are other features that could conceivably be included in the above list, one of which is the location of the ureter openings in the archosaurian cloacal cavity. Oliveira et al. (2004) noted that the paleognath *R. americana* and several tinamou species had ureters that opened into the coprodeum with the urodeum only receiving the vas deferens or oviduct. An identical layout was noted for the crocodilian *Caiman yacare* though this was not observed in any of the squamates studied. It was thus suggested that this may represent either an evolutionary relationship between the paleognath and crocodilian clades or in the alternative simply an adaptation to avoid mixing of seminae and urates in the cloaca.

3.6 Phylogeny of behavioural and reproductive traits

A cladogram detailing the most parsimonious evolutionary relationships among both extant and extinct archosaurs was chosen (after Varricchio et al. 1999) upon which the aforementioned 28 characters were mapped and analysed with PAUP 4.0b using a Bootstrap 50% majority-rule consensus rule. Unfortunately, having minimal data for most of the extinct taxa confounds such a study but when the characters were manually mapped onto the cladogram based on known or suspected appearances (Figure 16), the results indicate that the evolution of the derived neognath parental care system underwent at least five significant steps or stages in terms of reproductive structures, post-hatching parental behaviour and related adaptations.

Stage one

It appears that obligate oviparity, hard-shelled eggs, embryonic use of eggshell and the unique 'assembly line'

oviduct morphology are well-documented archosaurian synapomorphies. An intromittent, internally stored and extruding phallus is present in Archosauria with the notable exception of the neognatha and an equivalent organ was most likely present in male dinosaurs, a conclusion based not just on extant phylogenetic bracketing but also the most workable postures for copulation and their anatomical limitations. Construction of nests, pre-hatching parental care (nest guarding) and precocial self-feeding young are ancestral states in Archosauria, though post-hatching parental care becomes much more sophisticated in the derived neognath taxa. Female sperm storage is known for crocodilians and extant birds and in that respect was likely present in dinosaurs. Temperature-based gender determination is a standard crocodilian and chelonian trait, though the gender of all extant avian neonates is genetically fixed. It is interesting to note that neonate gender can be influenced in the megapode Australian brush-turkey (*Alectura lathami*) in which higher incubation temperatures produced females (Goth 2007), though this phenomenon may be unique to this particular clade. While this may well be ancestral, it is not possible to determine whether or not this character was present in any dinosaur as it simply cannot be tested for in extinct taxa.

Stage two

Integumentary structures have been identified and confirmed in the stem ceratopsid *Psittacosaurus* and the heterodontosaurid *Tianyulong*. Such protofeather-like filaments were previously considered to be exclusively

avian characters. It remains unclear as to whether or not the described integument evolved independently in these taxa or if this feature represents a true synapomorphy of Dinosauria.

Stage three

The Coelurosauria, notably *Troodon* and oviraptorids, demonstrate characteristics that are undoubtedly avian synapomorphies. These include unique eggshell microstructure, large eggs and clutches, monoautochronic ovulation and perhaps delayed incubation of embryos though this remains unclear (in regard to the latter, see discussion in Wesolowski 2004).

Stage four

Among extant Aves, the right ovary and its associated oviduct have become vestigial. Eggs are laid individually over a period of time in an open nest exposed to the elements and do not develop until subject to direct contact incubation from an adult. Furthermore, the eggs are rotated during the incubation period and a specialised structure called the chalazae holds the embryo in position to prevent damage.

Stage five

In Neoaves, the male phallus displays considerable variation for while it has been lost among neognatha taxa in favour of direct cloacal apposition, the organ is fully present in the Anseriformes though by contrast

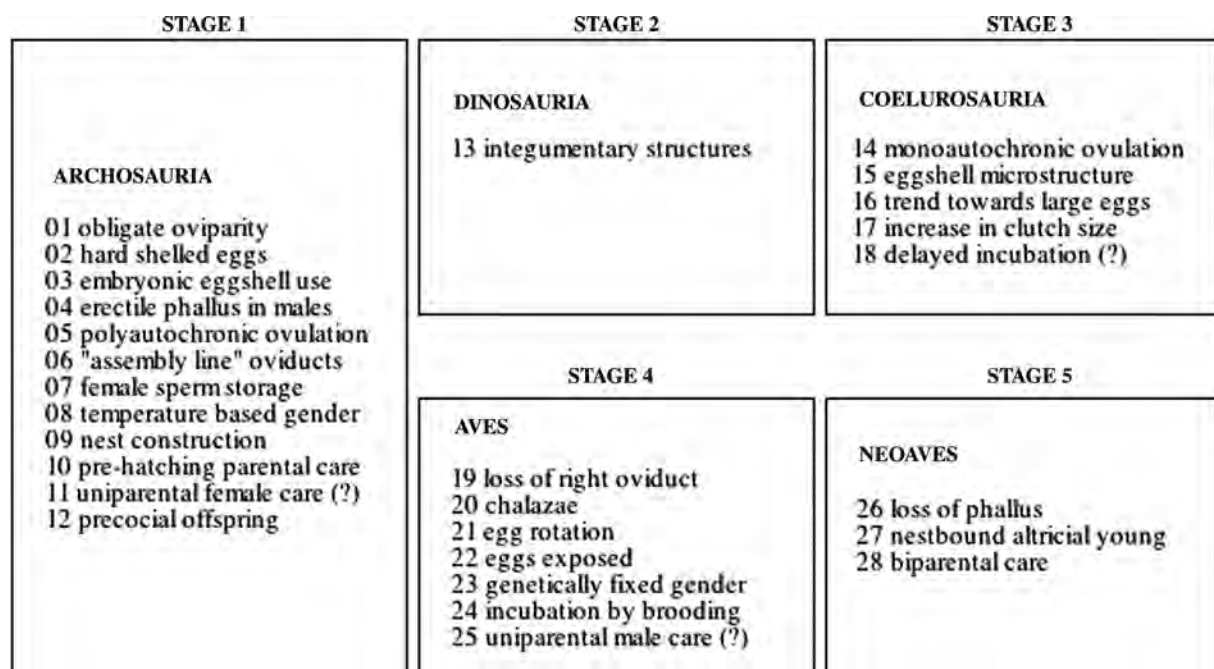


Figure 17. graphical representation of the hypothetical five evolutionary stages of neognath reproduction with associated characters.

remains erectile but non-intromittent in the Galliformes. Neognath neonates are distinct from the Galloanserae in that the former are hatch blind, featherless and are completely helpless, nest bound to the point where post-hatching care is intensive, long term and normally requires more than one parent. Among taxa in the latter group, neonates are largely self-feeding and leave the nest shortly after hatching. Parental care is further differentiated in Neoaves, with a strong bias towards female-only care among Galloanserae, whereas there is a trend towards extended biparental care and at least seasonal monogamy in Neognathae, both traits clearly a response to the unique care requirements of their offspring (see Figure 17 for a diagram of the five hypothetical steps.)

Many investigators have proposed parental care in some form as being an ancestral condition for the Archosauria (e.g. Varricchio et al. 1999; Burley and Johnson 2002; Prum 2002; Tullberg et al. 2002) with the common ancestor of crocodilians, dinosaurs and birds demonstrating at the very least female care. Therefore, the forms of post-hatching parental care observed in extant archosaurs are considered to be a homologous character. This study would appear to agree that female-only care was the ancestral archosaurian trait and the most parsimonious condition for extinct dinosaurs, with male-only care biased towards the paleognatha and biparental care common among neognatha. However, despite this apparent parsimony, further evaluation may raise questions as to the utility of employing crocodilian and avian parental care traits. In that regard, do the parental care modes of Crocodilia and Neoaves serve any relevance as a comparison to what might have occurred in dinosaurs?

Crocodilians are often considered to be examples of an exclusively female-only model of post hatching care, though it is important to note that both seasonal monogamy and biparental care occur in some species (Shine 1988; Coombs 1989). This appears to be influenced by low density population conditions (Lang 1987; Kofron 1991). The exclusively aquatic habitat of crocodilians (e.g. Trutneau and Sommerlad 2006) compared to the volant neognatha (e.g. Elphick et al. 2003) injects a further ecological confound. The guarding of eggs and young seen in extant archosaurs is behavioural routines that evolve easily, being both widespread and independently attained throughout vertebrate and invertebrate clades within which there are often minimal evolutionary relationships (see Clutton-Brock 1991). Moreover, an approximately 260 million year split between the basal common ancestor of both the crocodilian and avian lineages (e.g. Walker 1972; Norman 1985) only adds to the question as to whether any parental care modes observed between the two clades can be considered as synapomorphies or homoplasies. It is entirely plausible that the parental behaviours of extant archosaurs evolved independently

and such problems result in the 'female-only' ancestral care hypothesis being rejected.

All evidence to date indicates that the biparental origin of parental care was a trend that appeared in response to the unique attendance requirements of derived neognath hatchlings. There is nothing in the fossil record, whether it be mass accumulations or trace evidence, that would remotely indicate its presence in extinct archosaurs so the biparental origin hypothesis of avian care can be safely rejected on the basis of absence of supporting evidence. The male care origin hypothesis proposed by Wesolowski (1994) and Varricchio et al. (2008a) is confounded by the limitations of applying regression analysis to highly incomplete data-sets and by the resorption of medullary bone by incubating female birds. As there is currently no unequivocal method of verifying the sex of a dinosaur beyond the discovery of fossilised internal eggs, the hypothesis that male-only care had its origins among coelurosaurian theropods does not appear workable.

The classical view has long held that among bird 'female-only' care is limited to taxa with lek polygyny mating systems and 'male-only' care to polyandrous taxa (e.g. Silver et al. 1985). Owens (2002) argued that female-only care occurred in groups with high-density nesting with male-only care dominant in low-density nesting. It was further suggested that mode of parental care was associated with remating opportunities, which when abundant for both sexes favours female-only care and when rare for both sexes and particularly scarce for males favours male-only care. Therefore, sexual differences in remating chance act as a key factor in determining male-only care and classical polyandry in birds. However, in a detailed evaluation, Cockburn (2006) noted that in birds with female-only care the only significant correlation was with birds that fed primarily on nectar and fruit, both of which are heavily abundant, which renders male provisioning assistance of limited value. However, despite this strong correlation, there are taxa for which this approach yields an unsatisfactory explanation. Furthermore, it was effectively demonstrated that no common pattern exists between groups in which males are the predominant care providers and even the best correlate, highly precocial young, has its exceptions [see Cockburn (2006) for detailed discussions and examples]. Andersson (2005) concluded that a single hypothesis is unlikely to explain all extant cases of male-only care though noted that classical polyandry appears to be associated with factors such as a larger female body size and a habitat rich in food during the breeding season. There is no reliable indication that female coelurosaurian theropods demonstrated size dimorphism nor is it possible to recreate the intricacies of either an ecology or social dynamic from the fossil record. Any attempt to do so will be subject to such a variety of confounds as to be little more than speculation.

The preceding arguments about care models are all based on the explicit assumption that extinct archosaurs exhibited post-hatching parental care and in doing so overlook one key question: did parental care even occur after hatching? This fundamental question is one that is rarely considered in paleontology and deserves evaluation, for while there is evidence of at least occasional pre-hatching or nest-guarding behaviour in coelurosaurian theropods (e.g. Norell et al. 1995; Dong and Currie 1996; Varricchio et al. 1999), it is not known if post-hatching care was the exception or the norm among dinosaurs. The duration and nature of both crocodilian and basal avian parental care tend to differ considerably among taxa and it is just as likely that any post-hatching care in extinct taxa demonstrated similar variety. Possible post-hatching associations of adults and juveniles have been reported in *Psittacosaurus* (Meng et al. 2004), sauropods (Carpenter 1999) and the hypsilophodontid *Oryctodromeus* (Varricchio et al. 2007). However, there is no way of knowing if these represent parent–young interactions or some other as yet unknown social dynamic. Juvenile dinosaurs were unusual among terrestrial vertebrates for aggregating into what appear to be exclusive herds or groups for an extended period of time with no sign of adult supervision. This phenomenon is widespread, having been reported for Sauropodomorpha (Myers and Fiorillo 2009), Thyreophora (Galton 1982b; Currie 1989), Ornithopoda (Forster 1990), Ceratopsia (Weishampel et al. 2000; Mathews et al. 2009) and Ornithomimosauria (Kobayashi and Lu 2003; Varricchio et al. 2008b). Whether these were temporary or long term, seasonal or a specialised anti-predator defence is ambiguous, though the observation remains that such groupings are rare in extant archosaurs. By stark contrast, theropod dinosaurs apparently had no post-hatching parental attendance and extreme morphological differences between adult and juvenile (e.g. Varricchio et al. 2002; Rahut and Fechner 2005) strongly indicate resource partitioning as a means to deter competition between the generations.

An interesting lesson offered by the current fossil record, and one that appears to be frequently overlooked or played down by investigators, is the overall lack of evidence to be found of post-hatching care in dinosaurs. It is concluded here that extant archosaurs have little to offer in terms of insight. Virtually exclusive male-only care appears to represent a specialised adaptation in paleognath taxa and biparental care a response to super-altricial young in the neognatha, while crocodilians demonstrate a strong bias towards female care that may represent a clade-specific ecological or behavioural limitation. Current evidence indicates that extinct archosaurs employed very different reproductive strategies involving long term exclusively juvenile groups which appear to conform with resource partitioning models. Clear advantages of such behaviours are the ability to minimise potentially

disruptive competition between adult and offspring and as an anti-predator tactic, respectively. Actual discoveries of adult specimens associated with apparent neonates appear to represent specialised behaviours such as putative ‘creche’ minding (e.g. Meng et al. 2004) or fossorial adaptations (e.g. Varricchio et al. 2007). It has long been a rhetorical question as to why extinct dinosaurs were such a remarkably successful and geologically long lasting group of animals, though a lack of post-hatching care has, to the author’s knowledge, never been suggested. Offspring that require no post-hatching maintenance offer adults an opportunity for energy acquisition that would otherwise have been required to defend and provision to be redirected towards faster growth and increased fecundity, both traits which appear well expressed in the fossil record. Not only does this ‘minimal or no post-hatching parental care’ hypothesis shed light on the broad lack of evidence for the same in dinosaurs but offers a workable explanation as to why that might be.

Prum (2002) claimed ‘extensive parental care is primitive to archosaurs’ and implied that the more advanced aspects of extant avian care behaviours boasted an explicit coelurosaurian theropod origin, though this study would question such a conclusion. Behaviours unique to extant birds include direct contact brooding, superaltricial nest-bound neonates and an extended period of biparental post-hatching care, none of which have been satisfactorily shown in any extinct dinosaurian taxon. The aforementioned traits have been shown conclusively to be exclusive to neognatha (see Dial 2003) and the behaviours which are demonstrable for dinosaurs include both the construction and guarding of nests, neither of which can be considered ‘extensive’, as such behaviour is widespread throughout extant vertebrate and invertebrate clades. We thus return to the previously cited warning of Coombs (1982) who cautioned that choice of extant analogue can result in a subtle trap that encourages interpretations far beyond what can reasonably be concluded from the available data. This study has reinforced this advice. Birds, crocodilians and extinct dinosaurs must be treated as unique subjects and in that respect the popular term ‘non-avian theropod’ has been carefully avoided here, as the subtle connotation is that extant neognatha and extinct coelurosaurians are interchangeable in terms of behavioural and parental characteristics, a situation clearly unwarranted. Previous studies regarding avian parental care ancestry maintain a reliance on theoretical male–female interactions and mate choice models that are not subject to fossil preservation and therefore cannot be reliably tested. The problem of reliable gender determination in dinosaurs is absolutely critical and cannot be underestimated given how highly dependent the models are regarding putative gender roles. Further problems with cladistic theory and its application to paleontology only add to the complexity of such

investigations (e.g. Cronquist 1987; Pritchard 1994; Kluge 1997; Zherikhin 1998; James and Pourtless 2009). It can be concluded that of all three parental care hypotheses, none conform in a satisfactory manner with both fossil and trace evidence and as such the ancestral state remains unclear. This paper suggests an alternative 'minimal or no care' scenario for extinct dinosaurs that not only sheds light on the lack of demonstrable preservation of parental care traces, but also offers a workable alternative that may help to explain the extraordinary evolutionary success of these animals.

4 Summary

This paper has reviewed the current knowledge of both the reproductive characters and hypothetical socio-sexual behaviours of extinct archosaurs and in that respect several key observations and conclusions can be made:

- (1) Attempts to discriminate potential sexual dimorphism in dinosaurs are often troubled by very small sample sizes, preservation bias, ontogenetic change and possible geographic and temporal variations. However, as this phenomenon is common for both vertebrates and invertebrates, it is highly unlikely that dinosaurs should prove an exception.
- (2) There is currently no reliable method to determine gender from skeletal remains thus confounding theories concerning social structures and sexual selection. The use of haemal arch geometry to suggest the presence of hypothetical 'penile retractor muscles' as an indicator of gender has been refuted. Medullary bone has been offered as unequivocal evidence of dinosaur gender because in extant avians, it is used as a calcium reservoir for shelling eggs. Therefore, a fossil long bone found with medullary tissues would belong to a female, and the apparent lack of this tissue for oviraptorids associated with nests has been viewed as evidence that the attending adults were male. However, despite a promising outlook, there exist problems with this hypothesis and the most reliable test as to its possible utility would be an evaluation of the 'shelled egg' oviraptorid described by Sato et al. (2005) for evidence of putative medullary structures.
- (3) Cranial ornamentation is common among many dinosaur groups and most likely served in multiple functions such as interspecific signals, dominance badge displays, species-specific mating mechanisms, ritualised combat among males and mating signals along with subsequent speciation events.
- (4) Courtship behaviour in extant archosaurs involves complex vocal and visual displays, both of which may well have been present in dinosaurs, though such traits are difficult to evaluate in extinct organisms.
- (5) It is not really possible to reconstruct social structures for extinct archosaurs and any attempt would be purely speculative. However, trackways and monospecific mass assemblages appears, to strongly suggest herding behaviour and in that respect many sauropod, ceratopsid and hadrosaurid dinosaurs might have been gregarious, travelling in herds composed of both adult and subadult members. In stark contrast, there exists very little reliable evidence that suggests that theropods were highly social.
- (6) Fossil evidence and extant phylogenetic bracketing indicate that dinosaur reproductive anatomy was a unique combination of what is seen in extant archosaurs. Male dinosaurs almost certainly had a phallus which would likely be crocodilian in nature. However, as both the crocodilian and ratite phalli have a virtually identical layout and structure, the argument is somewhat moot. Female dinosaurs most likely had two functional oviducts and employed an 'assembly line' method of producing albumen and shelling eggs though in coelurosaurian theropods, trace evidence would indicate that only two eggs were produced at a time.
- (7) Extant models indicate that the most parsimonious sexual posture for dinosaurs is a variation of the reptilian 'leg over back' method with certain dinosaur groups employing modified positions for copulation due to either their sheer weight or the presence of dorsal spines and plates which would interfere with any attempt at dorsoventral mounting.
- (8) All dinosaurs demonstrated obligate oviparity due to specialisation of the extant archosaur female reproductive tract which does not allow for the extended retention of eggs required for evolutionary models of viviparity. Both extant and extinct archosaur eggshells have similarities that include a thick, hard shell composed of calcite crystals covered by numerous pores to allow for the diffusion of respiratory gases. The eggshell of coelurosaurian theropods has several unique avian features which include prismatic shell units and a squamatic ultrastructure.
- (9) Egg-laying strategies of dinosaurs appeared to fall into two distinct categories: those laid in buried clutches and those constructed above ground. Colonial nesting has been shown for titanosaurs sauropods, but not conclusively for any other dinosaur group. Theropods appear to nest exclusively alone.
- (10) Incubation of dinosaur eggs appears to have occurred via the decomposition of a vegetative cover or by burial in substrate. Scenarios of coelurosaurian theropods performing true avian style brooding with feathers and brood patches have been long popularised but have serious practical drawbacks. It is more parsimonious that such nests were left open to allow the ambient temperature to initiate develop-

mental stasis with the eggs being buried upon completion of the clutch.

- (11) There can be little doubt that pre-hatching egg attendance certainly occurred among coelurosaurian theropods, but substantive evidence for post-hatching care for any dinosaur group with the exception of the hypsilophodontids remains extremely poor. There is strong evidence for juvenile group formation in many dinosaurs, though it is unclear as to whether most were attended by an adult. Embryonic studies strongly suggest that dinosaur hatchlings were either precocious or superprecocious with theropods appearing to exhibit stark differences between the generations. This observation and that of extensive juvenile-only groupings strongly indicate a form of niche partitioning in which adult and offspring avoid conflict by exploiting very different resources, a hypothesis that has been poorly developed in the existing literature and clearly warrants a more detailed evaluation.
- (12) Birds, crocodilians and extinct dinosaurs must be treated as unique subjects because choice of extant analogue often results in interpretations that extend far beyond what can be concluded from the available data. This study has demonstrated that the use of extant archosaurs as explicit behavioural models for their extinct relations is wrought with confounds and complications. No current parental care hypothesis conforms with both fossil and trace evidence and as such the ancestral state for Neornithes remains unclear.

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