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Androgynous rex – The utility of chevrons for determining the sex of crocodilians and non-avian dinosaurs

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Abstract

The sex of non-avian dinosaurs has been inferred on numerous occasions using a variety of anatomical criteria, but the efficacy of none has been proven. Nearly 50 years ago Romer suggested that the cranial-most or first chevron in the tails of some reptiles, including crocodilians, is sexually dimorphic. Recent work on this subject purportedly substantiated that the female first chevron articulates in a more caudal position than in males. Furthermore, it was concluded that this element is shorter in females. These phenotypic attributes theoretically provide a broader cloacal passageway for eggs by ovipositing females and a greater attachment area for male "penile retractor muscles". Because theropod dinosaurs such as *Tyrannosaurus rex* presumably show similar variation in chevron anatomy, the same criteria has been advocated for sexing dinosaurs. We tested the neontological model for the chevron sexual dimorphism hypothesis using a skeletonized growth series of American alligators (*Alligator mississippiensis*) of known sex. No statistical support for the hypothesis was found. Furthermore, analysis of a diversity of crocodilian taxa from museum collections revealed similar findings suggesting the alligator results are not taxon specific. Study of well-preserved tyrannosaurid dinosaurs in museum collections showed nearly invariant chevron positioning like that seen in crocodilians. This suggests the usefulness of chevron anatomy for sexing dinosaurs is tenuous.

Keywords: Sexual dimorphism; Dinosauria; Tyrannosauridae; Crocodylia; Individual variation

Introduction

Establishing dependable means to determine the sex of non-avian dinosaurs is one of the most sought after goals in dinosaur vertebrate paleontology (Brown and Schlaikjer, 1943; Dodson, 1975, 1976; Thulborn, 1974; Colbert, 1989; Raath, 1990; Chapman, 1990; Weishampel and Chapman, 1990; Carpenter, 1990; Lehman, 1990; Chinsamy, 1990; Larson, 2002; Schweitzer et al., 2005; Sato et al., 2005). This capacity would have important ramifications for understanding the paleobiology and taxonomy of dinosaurs. For example, it could lead to the identification and timing of display attributes reflecting sex and reproductive maturity. Further, it could be used to conduct more sophisticated studies of dinosaur population demographics. Finally, knowledge about sex-related attributes could aid paleontologists in making and testing taxonomic assessments, thereby ensuring that members of the same species are not mistaken for different taxa.

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Skeletal indices that directly reflect differences in the reproductive organs hold considerable promise for attaining this goal. Notably, Romer (1956) reported finding just such a sex-specific attribute in the tailbones of crocodilians, the living sister group to the Dinosauria. He specified that the cranial-most chevron or haemal arch (the first of a series of wishbone-shaped bones located just caudal to the cloaca and ventral to the vertebral centra through which the haemal artery and vein pass; Fig. 1) shows positional variation between males and females. Romer posited that such differences could be used to sex extinct reptiles, but failed to provide data in support of his conclusion. Subsequent dissections of American alligators (*Alligator mississippiensis*) and unspecified crocodilians, as well as examination of *A. mississippiensis* in museum skeletons, seemed to clarify that this element is indeed sexually dimorphic (Larson and Frey, 1992; Larson, 1994, 1998, 2002; Powell, 2000). Specifically, Larson (1994) reported that the first chevron articulates between the second and third caudal vertebrae in males, and between the third and fourth caudal vertebrae in females (Fig. 1). Powell (2000) on the other hand claimed that the same element resides between the first and second caudal vertebrae in males, and between the second and third in females. Both researchers concurred that the first chevron is considerably shorter in females (typically 28% that of males, Larson, 1994; typically 50% that of males, Powell, 2000). The latter generalization presumably escaped Romer's attention (Larson, 1994), although he did acknowledge that the first chevron is relatively short and incompletely developed in some specimens (Romer, 1956).

Why might such sexual differences exist in crocodilians? It was posited that they reflect reproductive function (Larson, 1994; Powell, 2000). Specifically, the female phenotype provides a broader cloacal passageway for eggs, whereas that of the male affords greater attachment surfaces for the "penile retractor muscles" (*sensu* Larson, 1994, 1998, 2002; a misnomer in that these muscles, the mm. transversus laterales pars dorsalis and ventralis, are found in both sexes where they likely act to pull the vent caudally as well as to close it, and their role in penile retraction is untested, see Powell, 2000).

Preliminary examination of skeletons from *Tyrannosaurus rex* and Troodontidae suggested that similar chevron variability and dimorphism occurred in dinosaurs. Larson (1994) concluded that the first chevron articulates between the second through fourth caudal vertebrae in *T. rex* (see Fig. 10, p. 153 in Larson, 1994; Fig. 2), whereas the sixth sacral through second caudal vertebrae are involved in troodontids (Larson, 1994, 1998, 2002). Given these positive results, the use of chevron position and length data to determine the sex of theropods was advocated (Larson, 1994; Powell, 2000).

The senior author of this paper noted discrepancies from these findings while dissecting several *A. mississippiensis* specimens for use as teaching specimens. Both male and female representatives had comparably proportioned first chevrons, and these articulated only

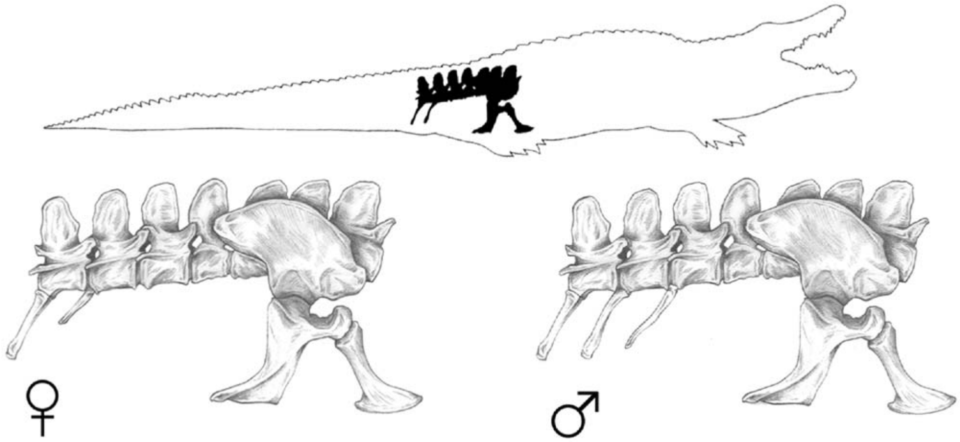

Fig. 1. Hypothetical *Alligator mississippiensis* pelves and proximal caudal vertebrae showing positional and proportional chevron sexual dimorphism. The chevron sexual dimorphism hypothesis of Larson (1994) posits that the first chevron (the cranial-most skeletal element located ventral to the caudal vertebrae) articulates between the third and fourth caudal vertebrae in females (left) and is considerably shorter than the second chevron. In males (right) the first chevron articulates more cranially between the second and third caudal vertebrae and this element is nearly the same length as the second chevron. Note that the female phenotype has a larger gap between the pelvic bones and the first chevron. Theoretically, this results in a broader cloacal passageway through which eggs can pass during oviposition. The longer first chevron in the male phenotype presumably provides a greater attachment area for "penile retractor muscles" (*sensu* Larson, 1994). (*Note*: the chevron sexual dimorphism hypothesis for crocodilians of Larson (1994) was incorrectly described by Brochu (2003) with the first chevron occurring between the first and second caudal vertebrae in males and between the second and third caudals in females. The hypothesis of Powell (2000), however, fits this description.) Illustration by Ashley Eggers.

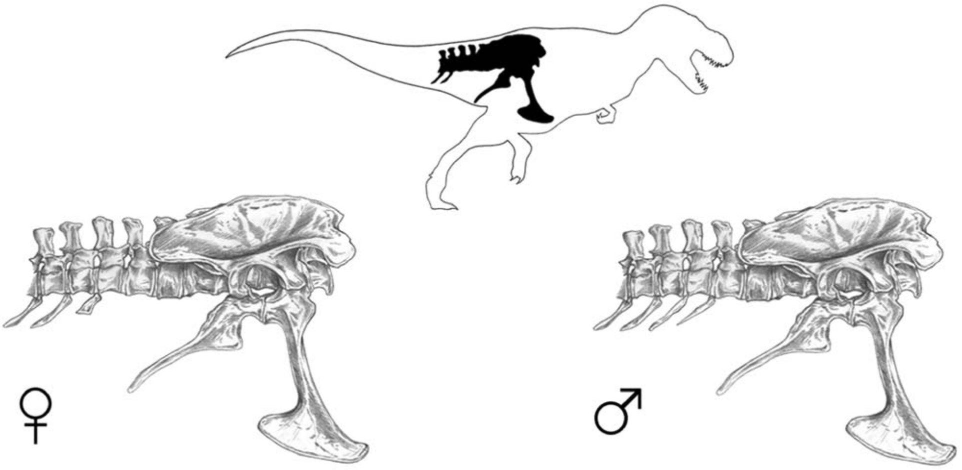

Fig. 2. Hypothetical *Tyrannosaurus rex* pelves and proximal caudal vertebrae showing positional and proportional chevron sexual dimorphism. Using crocodilians as a model, it has been posited that chevron sexual dimorphism occurs in theropod dinosaurs such as *T. rex* (Larson, 1994, 1998, 2002). In this taxon, the first chevron in females (left) presumably articulates between the third and fourth caudal vertebrae and is shorter than the second chevron. In males (right) the first chevron is more cranially situated between the second and third caudal vertebrae and is nearly the same length as the second chevron. (*Note*: the chevron sexual dimorphism theory for tyrannosaurs of Larson (1994) was incorrectly described by Brochu (2003) with the first chevron occurring between the first and second caudal vertebrae in males and between the second and third caudals in females. Brochu concluded that FMNH PR 2081 fit the purported male phenotype, when in fact it positionally conforms to neither in the original hypothesis. Nevertheless, the first chevron is decidedly shorter than the second. This led Larson (2002) to deduce that FMNH PR 2081 was likely female). Redrawn by Ashley Eggers from an illustration by Dorothy Sigler Norton in Larson (1994).

between the second and third caudal vertebrae. This spurred an extensive literature search on crocodilian haemal arch anatomy that revealed four additional references to chevron position and/or proportions in which members of both sexes were presumably examined (Reese, 1915; Chaisson, 1962; Kardong and Zalisko, 2002; Brochu, 2003). Each mentioned that the first chevron articulates between the second and third caudal vertebrae (although Fig. 5.11, p. 47 in Kardong and Zalisko (2002) shows it between the first and second caudals). Brochu (2003) acknowledged that variance from this character state can occur, but for reasons that were not specified, offered the opinion this was due to individual variation rather than sex-related influences. Reese (1915) specified that chevron lengths diminish cranio-caudally but failed to mention the first element being attenuated relative to the second.

The developmental literature revealed additional information incongruous with the chevron sexual dimorphism hypotheses. Sex determination in crocodilians is temperature dependent. In *A. mississippiensis* the thermosensitive period occurs between embryonic developmental stages 21–24 (30–45 days post-oviposition; Lang and Andrews, 1994). The senior author's examination of cleared and stained *A. mississippiensis* specimens in the Field Museum, Chicago (FMNH 250645, 250646, 250648, 250651) showed that chevron chondrogenesis is complete by stage 18 (day 26) when the embryos are still sexless (Fig. 3). Furthermore, the first haemal arch anlage articulates between the second and third caudal vertebrae in three of the specimens. A rudimentary first chevron is located between the first and second caudal vertebrae in a fourth individual. Hence, complete dilapidation of one or more elements would be required for these specimens to assume the purported female phenotype in the chevron sexual dimorphism hypotheses of Romer (1956) and Larson (2004). For the majority of these embryos to assume the male phenotype described by Powell (2000), a new chevron would have to develop between the first and second caudal vertebrae after all others had formed. Both are processes that have never been reported in *A. mississippiensis* despite extensive studies of skeletal development (e.g. Ferguson, 1981; Allstead and Lang, 1995).

Finally, the same 14 *A. mississippiensis* skeletal specimens in the United States National Museum, Washington, DC (USNM) used by Powell (2000) to purport skeletal sexual dimorphism were examined. Problems were found owing to errors in data transfer that cast doubt about this conclusion. Namely, four specimens used as representatives of one or the other sex had been accessioned in the museum records as being of unknown sex (USNM 209887, 211227, 211228, 209897), a female (USNM 312674) was reported as being male, and one specimen (USNM 209887), reportedly used in an axial skeletal analysis in the study, consists solely of a skull.

Collectively, these discrepancies warranted reanalysis to determine if haemal arch sexual dimorphism truly occurs in crocodilians and can be used as a model to

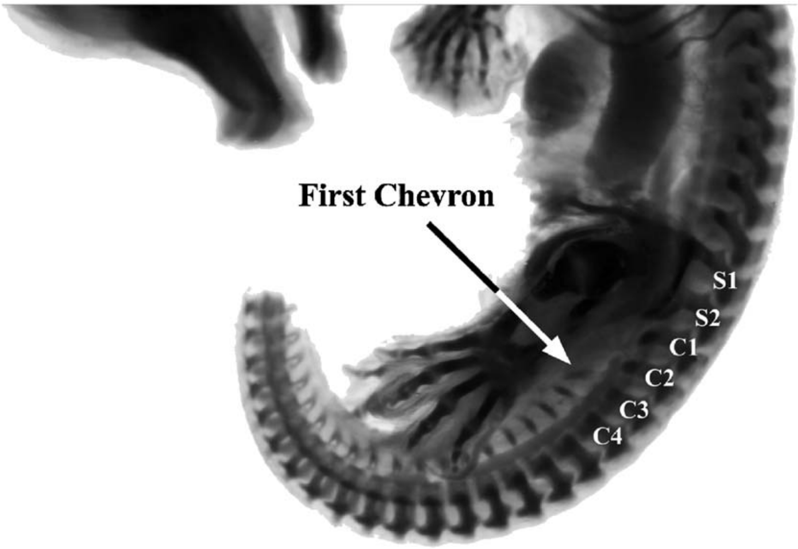

Fig. 3. Cleared and stained, sexually undifferentiated *A. mississippiensis* embryo showing proximal chevrons. This specimen FMNH 211228 is a stage 18 (day 26) embryo and hence was sexually undifferentiated at the time of death (Allstead and Lang, 1995). All chevrons in this specimen are chondrified (blue), and the first haemal arch (arrow) occupies a position between the second and third caudal vertebrae (designated as C2 and C3). Complete dilapidation of this element would be required for this specimen to assume the purported female phenotype in the chevron sexual dimorphism hypotheses of Romer (1956) and Larson (1994). Addition of a haemal arch between the first and second caudal vertebrae would be required for it to assume the purported male phenotype in the hypothesis of Powell (2000).

infer the sex of theropod dinosaurs. We conducted a three-part study to address these issues. First we acquired, skeletonized, and studied a growth series (juvenile through adult) of *A. mississippiensis* in which specimen sex was determined with certainty. We subjected these data to statistical analysis to explicitly answer the following question: Do first chevrons in *A. mississippiensis* show statistically significant differences in position and length relative to sex? Next, we examined skeletonized museum specimens of known sex representing a phylogenetic diversity of extant crocodilians. We used this to infer whether the patterns found for *A. mississippiensis* are generally applicable to the Crocodylia. Finally, since the tyrannosaurid *T. rex* served as the primary model for using chevrons to determine the sex of dinosaurs, direct examinations and reviews of the literature were made on this and other tyrannosaurs to infer whether chevron variability is comparable to that seen in crocodilians.

Materials and methods

Thirty-six wild-caught *A. mississippiensis* specimens were obtained for study through a licensed State of Florida nuisance alligator control agent. All specimens were captured in Gadsen, Seminole, or Jackson counties in northern Florida, USA. The sample included 17 females ranging in size from 1.52 to 2.64 m in total length (TL) and 19 males 1.52–3.35 m TL (Table 1). TL was measured to the nearest 1 cm for each individual (Table 1). The sex of each specimen was determined through probing of the cloaca manually (Brazaitis, 1968). The animals' axial regions, spanning from the sacral through proximal caudal regions, were removed and placed in covered pits, where they were partially buried in sand. The soft substrate served to keep all of the bones, including the diminutive chevrons, articulated. Naturally occurring dermestid beetles consumed the adhering flesh over periods of at least 2 months. Following exhumation, the specimens were accessioned into the collection of the Florida State University Museum, Tallahassee.

The location of the first chevron in each specimen was recorded. The TLs of the first and second caudal chevrons were measured perpendicularly from the bifid, proximal base of the bones to their pointed distal apex. These measurements were made to the nearest 0.1 mm (Table 1). Two analyses of covariance (ANCOVA) were used to test for sexually related differences in chevron morphology. First, to see if males have first chevrons of a different length than same-sized females, the length of the first chevron was compared between the sexes with TL as the covariate. Second, to see if proportional differences in relative first chevron length exist between sexes, the length of the second chevron was compared with the length of the first chevron as the covariate.

The skeletal collections of the USNM of Natural History, Washington, DC, Florida Museum of Natural History, Gainesville (FLMNH), and The Natural

Table 1. Sex, size, and chevron measurements for wild-caught northern Florida *Alligator mississippiensis*

Specimen #	Sex (M/F)	Total length (cm)	First chevron articulation	First chevron length (mm)	Second chevron length (mm)
FSUM 5000	M	152	C2/C3	32.5	34.0
FSUM 5001	M	160	C2/C3	33.2	34.6
FSUM 5002	M	184	C2/C3	46.4	50.0
FSUM 5003	M	198	C2/C3	34.9	46.8
FSUM 5004	M	213	C2/C3	42.2	44.7
FSUM 5005	M	216	C2/C3	39.5	49.9
FSUM 5006	M	221	C2/C3	46.2	48.7
FSUM 5007	M	224	C2/C3	58.2	56.3
FSUM 5008	M	234	C2/C3	52.8	55.1
FSUM 5009	M	241	C2/C3	36.4	53.8
FSUM 5010	M	244	C2/C3	69.1	68.1
FSUM 5011	M	244	C2/C3	57.2	60.1
FSUM 5012	M	244	C2/C3	42.4	60.6
FSUM 5013	M	246	C2/C3	46.0	60.0
FSUM 5014	M	251	C2/C3	46.5	61.2
FSUM 5015	M	251	C2/C3	57.6	64.9
FSUM 5016	M	282	C2/C3	46.1	60.7
FSUM 5017	M	325	C2/C3	70.1	80.0
FSUM 5018	M	335	C2/C3	74.6	78.1
FSUM 5019	F	152	C2/C3	28.4	31.9
FSUM 5020	F	182	C2/C3	47.0	47.0
FSUM 5021	F	184	C2/C3	46.4	50.0
FSUM 5022	F	187	C2/C3	43.0	45.0
FSUM 5023	F	193	C2/C3	45.2	45.9
FSUM 5024	F	195	C2/C3	40.8	46.9
FSUM 5025	F	195	C2/C3	41.5	45.8
FSUM 5026	F	198	C2/C3	54.0	54.0
FSUM 5027	F	203	C2/C3	43.8	52.4
FSUM 5028	F	205	C2/C3	44.2	48.3
FSUM 5029	F	205	C2/C3	48.0	50.0
FSUM 5030	F	208	C2/C3	49.0	50.0
FSUM 5031	F	212	C2/C3	47.4	48.5
FSUM 5032	F	213	C2/C3	29.4	45.7
FSUM 5033	F	241	C2/C3	59.4	59.5
FSUM 5034	F	251	C2/C3	48.9	60.9
FSUM 5035	F	264	C2/C3	59.3	75.7

History Museum, London (BMNH) were examined for crocodilian specimens of known sex from which chevron positions could be studied. Thirty-three specimens were found to conform to these criteria (16 males and 17 females; Table 2). The location of the first chevron attachment points was determined either through observation of the element in articulation or from attachment facets (Table 2). Chevron length was not measured since the sample sizes were too small to make statistically informative sexual comparisons within species.

Tyrannosaur specimens with well-preserved proximal tail regions in the Royal Tyrrell Museum of Paleontology, Drumheller, American Museum of Natural History, New York (AMNH), and The Field Museum, Chicago (FMNH) were examined by the senior author to determine proximal chevron articulation points. In addition, the publications of Lambe (1917) showing National Museum of Canada, Ottawa specimens, Gradzinski (1970) showing Paleobiological Institute of the Polish Academy of Sciences, Warsaw (ZPAL) specimens, and Horner and Lessem (1993) showing Museum of the Rockies, Bozeman (MOR) specimens, were examined. In total, seven tyrannosaurs representing three species were utilized (Table 3). Of these, three had been found with the first chevron in place. The rest had been placed according to the number of chevrons that were found, the number of unoccupied intercentral spaces, and their best fit on the haemal facets (e.g. Brochu, 2003), the latter of which were found to be considerably less distinctive than in crocodilians. Thus, conclusions about the typical condition in tyrannosaurs made here are tentative (Table 3). Measurements of chevron length were not made because: (1) some specimens were on public display and thus not directly

Table 2. Sex and first chevron articulation points for a diversity of crocodylian taxa

Taxon	Specimen #	Sex (M/F)	First chevron articulation	Comments
Alligator mississippiensis	USNM 209866	M	C2/C3	None
	USNM 313409	M	C2/C3	None
	USNM 209883	F	C2/C3	None
	USNM 209896	F	C2/C3	None
	USNM 291916	F	C2/C3	None
	USNM 312674	F	C2/C3	None
	USNM 312673	F	C2/C3	None
	USNM 312680	F	C2/C3	None
	USNM 312681	F	C2/C3	None
Alligator sinensis	FLMNH 105540	M	C2/C3	None
	FLMNH 67829	F	C1/C2	First chevron = just rudiments of base
Paleosuchus trigonatus	USNM 30252	M	C2/C3	None
	USNM 30060	M	C1/C2	First chevron normal in morphology
	NMNH 213705	F	C2/C3	None
Caiman crocodilus	FLMNH 19067	F	C1/C2	First chevron has an incomplete ramus
	FLNMH 45439	F	C2/C3	None
Melanosuchus niger	USNM 213704	M	C2/C3	None
Crocodylus acutus	USNM 247943	M	C2/C3	None
	FLMNH 56580	M	C2/C3	None
	FLMNH 63930	F	C2/C3	None
	FLMNH 98068	F	C2/C3	None
	FLNMH 56428	F	C2/C3	None
Crocodylus mindorensis	USNM 252670	F	C2/C3	None
Crocodylus niloticus	BMNH 1969.1565	M	C2/C3	None
	FLMNH 54812	M	C2/C3	None
C. porosus/siamensis hybrid	FLMNH 69364	M	C2/C3	None
Crocodylus siamensis	FLMNH 71182	F	C2/C3	None
Tomistoma schleggii	USNM 052972	M	C2/C3	None
	FLMNH 107493	M	C2/C3	None
	FLMNH 54210	M	C2/C3	None
	FLMNH 84888	F	C2/C3	None
Gavialis gangeticus	FLMNH 70592	M	C2/C3	None
	FLMNH 70592	M	C2/C3	None

accessible, (2) in some cases the chevrons were partially reconstructed, (3) sex was unknown, and (4) sample sizes were too small to allow meaningful statistical tests for dimorphism. The taxon designations of Currie (2003) were used to refer to these specimens.

Results

We found that the first chevron articulates between the second and third caudal vertebrae in all 36 (17 female and 19 male) northern Florida *A. mississippiensis* specimens (Table 1). The length of the first chevron in these specimens shows considerable intra-sex variation with respect to TL (Fig. 4). Statistical analysis indicated that the length of the first chevron is not significantly different between the sexes (ANCOVA: $F_{3,35} = 0.927$, $P = 0.343$). Also, the length of the second chevron relative to the length of the first chevron does not differ between the sexes (ANCOVA: $F_{3,\,35} = 2.118$, $P = 0.155$; Fig. 5).

The first chevron was found to articulate between the second and third caudal vertebrae in 30 (14 female and 16 male) of 33 museum specimens that were used to represent crocodilian phylogenetic diversity (Table 2).

Table 3. Tyrannosaurid first chevron articulations

Taxon	Specimen #	First chevron articulation	Notes
Tyrannosaurus rex	FMNH PR 2081	C1/C2	*Source*: Brochu (2003) and examined by GME
	MOR 555	C2/C3?	*Source*: Horner and Lessem (1993) and D. Varricchio (pers. comm.)
Tarbosaurus baatar	ZPAL I/3	C1/C2	Found with first chevron in articulation. *Source*: Gradzinski (1970)
Gorgosaurus libratus	RTMP 99.33.1	C1/C2	Found with first chevron in articulation and examined by GME
	FMNH PR 2211	C1/C2	Found with first chevron in articulation and examined by GME
	NMC 2120	C1/C2	*Source*: Lambe (1917)
	AMNH 5664	C2/C3?	Based on mount

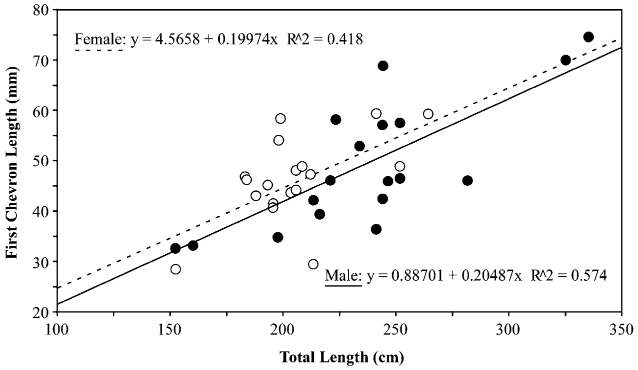

Fig. 4. First chevron length versus total length in male and female *Alligator mississippiensis.* Note that both male and female specimens show considerable variation in first chevron length with respect to body size. Analysis of covariance revealed that the sexes are statistically indistinguishable, which indicates that sex cannot be inferred from the relative length of the first chevron in this taxon.

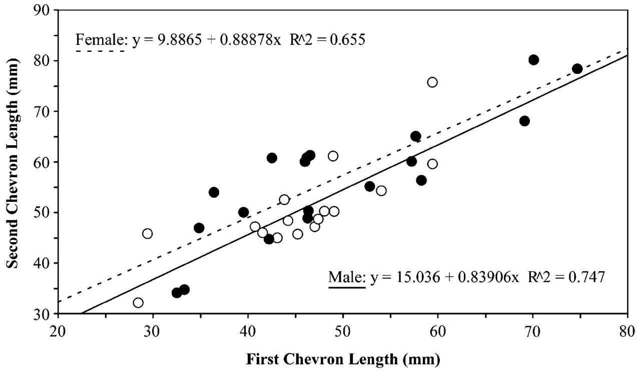

Fig. 5. Second chevron length versus first chevron length in male and female *Alligator mississippiensis.* Note that both male and female specimens show considerable variation in relative chevron proportions. Analysis of covariance revealed that the sexes are statistically indistinguishable, indicating that sex cannot be inferred from the relative length of chevrons in the cranial-most haemal arches.

The first chevron is located between the first and second caudal vertebrae in three other specimens (Table 2). Notably, in two of these the first chevron shows only rudimentary development (Fig. 6). Furthermore, in all three of these specimens there is at least one member of the same species (two of the same sex) showing the articulation between the second and third caudal vertebrae (Table 2).

In five of seven tyrannosaurid specimens that were studied, the first chevron appeared to definitively articulate between the first and second caudal vertebrae (Table 3). Conversely, the skeletal mount of one *Gorgosaurus libratus* individual (AMNH 5664) shows this element residing between the second and third caudal vertebrae. Information from the collector's (C.H. Sternberg) field notes on file at the museum and notes about the preparation of this individual (Matthew and Brown, 1923) failed to reveal whether the chevrons were actually found in articulation or if haemal facet locations were used as criteria for their placement (C. Mehling, personal communication to GME). Furthermore, it was not possible to directly observe the facets since the specimen is panel mounted. All other AMNH tyrannosaur mounts (AMNH 5428 [= USNM 12814], 5458, 5027) show comparable chevron positioning despite having tails that were considerably more incomplete. Given this, it is feasible that the chevrons of AMNH 5664 were mounted in their present position by institutional convention rather than anatomical criteria garnered from the specimen (also see Holtz, 2004). In situ photographs of *T. rex* specimen MOR 555 (unnumbered figure, p. 47 in Horner and Lessem, 1993) shows a chevron residing between the second and third caudal vertebrae. Direct examination of the vertebrae (D. Varricchio, personal communication to GME) revealed haemal facets in this same position but not in positions located more cranially. However, the first caudal vertebra shows poorer preservation and, as noted

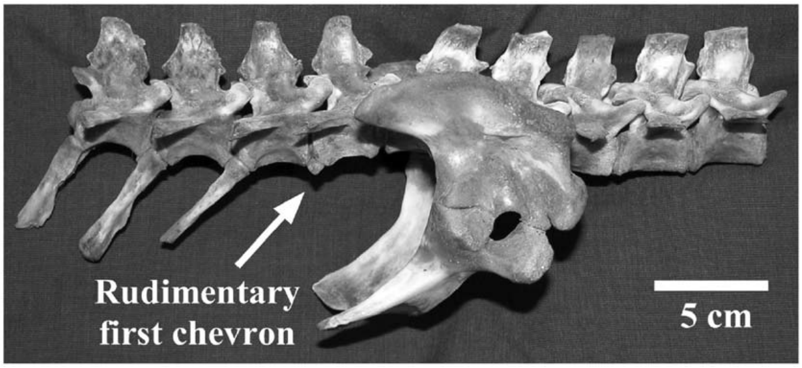

Fig. 6. Pelvis and associated vertebrae from a female specimen of *Alligator sinensis* showing rudimentary first chevron. The specimen (FLMNH 67829) shows vestiges of a first chevron between caudal vertebrae C1/C2. The present research suggests that this position for a first chevron is uncommon and aberrant among crocodilians.

previously, tyrannosaur haemal facets are considerably less distinctive than those in crocodilians. Given these considerations, the articulation point of the first chevron in this specimen was not established with certainty.

Discussion

The sex of dinosaurs has been inferred on numerous occasions based on a diversity of criteria including body size derived from the robustness of individual elements (Colbert, 1989; Raath, 1990; Weishampel and Chapman, 1990; Carpenter, 1990), horn-core length and/or curvature (Dodson, 1976; Lehman, 1990), crest development (Dodson, 1975, 1976; Lehman, 1990), cranial rugosity (Brown and Schlaikjer, 1943; Chapman, 1990; Larson, 2002), caniniform tooth proportions (Thulborn, 1974), hip width (Larson, 2002), ischial angulation (Carpenter, 1990), pelvic tunnel dimensions (Larson, 2002), and bone histology (Chinsamy, 1990; Schweitzer et al., 2005), just to name a few. Unfortunately, compelling evidence in the form of statistically supported osteological correlates indisputably reflecting sex has not been presented in support of any of these methods. Therefore, we cannot state with conviction that the sex of any dinosaur specimen is known with certainty – aside from a lone oviraptorid found with eggs within the pelvic cavity (Sato et al., 2005).

The rediscovery of Romer's (1956) sex-specific correlate, in the form of chevron attachment points, and follow-up work suggesting that chevron proportions also reflect sex (Powell, 2000; Larson and Frey, 1992; Larson, 1994, 1998, 2002), represented a promising direction for determining the sex of dinosaurs. Extant avian dinosaurs (birds) lack chevrons (Powell, 2000), but their presence in crocodilians opened the door to outgroup analysis using a living taxon as a model from which a second-order phylogenetic inference might be drawn (Witmer, 1994). However, the results of the present analysis provide no support for the hypothesis that these aspects of chevrons have utility for sexing crocodilians. In 100% (36/36) of the mixed sex (19 male:17 female) northern Florida, *A. mississippiensis* specimens the first chevron was invariably found between the second and third caudal vertebrae. This result clearly contradicts contentions that positional sexual dimorphism exists in crocodilians. Further evidence damning these hypotheses includes comparable chevron location in 91% (30/33) of the mixed-sex (16 male:17 female) specimens used to represent crocodilian diversity. This strongly suggests that the results for *A. mississippiensis* hold true throughout the Crocodylia and represent the plesiomorphic character state for the clade. We suspect that cases of atypical first chevron articulation points are the result of individual rather than sex-specific variation as Brochu (2003) first suggested. Evidence for this includes the rarity of such occurrences, the tendency for the elements to be diminutive and/or deformed, and the presence of such variation in both males and females.

Like the positioning of the haemal arches, analysis of chevron length and proportions in the 36 northern Florida *A. mississippiensis* specimens did not support hypotheses that these criteria can be used to determine the sex of specimens/individuals of this taxon. Individual variation of chevron dimensions exceeded sexual differences across body size and as such cannot be used to differentiate between males and females.

An obvious question raised is: Why have previous studies concluded that *A. mississippiensis* chevrons are sexually dimorphic? As mentioned earlier, some results may be attributable to the introduction of error through simple misrecordings of the sex of specimens from museum records. In addition, we suspect that the practice of not fully skeletonizing specimens and unfamiliarity with the anatomy may have led to element and attachment point misidentifications. Finally, it is feasible that small sample sizes, coupled with the effects of individual variation, may have influenced the outcome of previous works.

The limited evidence presented here points to tyrannosaurs being similar to crocodilians in having first chevrons that typically occupy a characteristic position on the tail (Table 3). This goes hand in hand with Larson's (1994) observation of variance in the length of this element between individuals shown here to also occur in crocodilians. All in all, our findings provide reason to suspect that variance in chevron position and proportions in tyrannosaurs reflects individual variation (and perhaps mistakes made while mounting skeletons), rather than sexual anatomical differences.

On a broader note, approaches such as those used here, where techniques and philosophies garnered from a number of disciplines (developmental biology, comparative evolutionary morphology, reproductive biology, vertebrate paleontology, etc.) were employed to gain new scientific insight, trace their roots to the integrative biology movement of the 1990s. This was spearheaded by Marvalee Wake (2000) who first realized the great potential of this approach. As several recent articles in *National Geographic* (Achenbach, 2003), *New Scientist* (Gosline, 2005), and *Newsweek* (Adler, 2005) attest, no discipline has benefited more than vertebrate paleontology from their efforts. We stand to make unprecedented advancements towards a comprehensive understanding of vertebrate evolutionary biology as a result.

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References

Achenbach, J., 2003. Dinosaurs come alive. National Geographic, March, pp. 2–33.

Adler, J., 2005. Buried treasure. Newsweek, June 27, pp. 44–52.

Allstead, J., Lang, J.W., 1995. Sexual dimorphism in the genital morphology of young American alligators, *Alligator mississippiensis*. Herpetologica 51, 314–325.

Brazaitis, P.J., 1968. The determination of sex in living crocodilians. Br. J. Herpetol. 4, 54–58.

Brochu, C.A., 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. Soc. Vert. Paleo. Mem. 7, 1–138.

Brown, B., Schlaikjer, E.M., 1943. A study of the troodont dinosaurs with the description of a new genus and four new species. Am. Mus. Novit. 1169, 1–15.

Carpenter, K., 1990. Variation in *Tyrannosaurus rex*. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 141–145.

Chaisson, R.B., 1962. Laboratory Anatomy of the *Alligator*. WC Brown, Dubuque.

Chapman, R.E., 1990. Shape analysis in the study of dinosaur morphology. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 21–42.

Chinsamy, A., 1990. Physiological implications of the bone histology of *Syntarsus rhodesiensis* (Saurischia, Theropoda). Palaeont. Afr. 27, 77–82.

Colbert, E.H., 1989. The Triassic dinosaur *Coelophysis*. Museum of Northern Arizona Bulletin 57. Museum of Northern Arizona, Flagstaff.

Currie, P.J., 2003. Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada. Acta Palaeontol. Pol. 48, 191–226.

Dodson, P., 1975. Taxonomic implications of relative growth in Lambeosaurine hadrosaurs. Syst. Zool. 24, 37–54.

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

Ferguson, M.W.J., 1981. The reproductive biology and embryology of the crocodilians. In: Gans, C., Billet, F.S. (Eds.), Biology of the Reptilia: Development, vol. 12. Academic Press, New York, pp. 329–498.

Gosline, A., 2005. Reanimators. New Scientist, May 21, pp. 47–51.

Gradzinski, R., 1970. Sedimentation of dinosaur-bearing Upper Cretaceous deposits of the Nemegt Basin, Gobi Desert. Palaeontol. Pol. 21, 147–229.

Holtz Jr., T.R., 2004. Tyrannosauroidea. In: Weishampel, D.B., Dodson, P., Osmolska, H. (Eds.), The Dinosauria, second ed. University of California Press, Berkeley, pp. 111–150.

Horner, J.R., Lessem, D., 1993. The Complete *T. rex*. Simon and Schuster, New York.

Kardong, K.V., Zalisko, E.J., 2002. Comparative Vertebrate Anatomy: A Laboratory Dissection Guide, third ed. McGraw-Hill, Boston.

Lambe, L.M., 1917. The Cretaceous theropodus dinosaur *Gorgosaurus*. Mem. Geol. Surv. Can. 100, 1–84.

Lang, J.W., Andrews, H.V., 1994. Temperature-dependent sex determination in crocodilians. J. Exp. Zool. 270, 28–44.

Larson, P.L., 1994. Tyrannosaurus sex. In: Rosenberg, G.D., Wolberg, D.L. (Eds.), Dino Fest. The Paleontological

Society Special Publication 7. The Paleontological Society, Knoxville, pp. 139–155.

Larson, P.L., 1998. The theropod reproductive system. Gaia 15, 389–397.

Larson, P.L., 2002. Rex Appeal. Invisible Cities Press, Montpelier.

Larson, P.L., Frey, E., 1992. Sexual dimorphism in the abundant Upper Cretaceous theropod, *Tyrannosaurus rex*. J. Vert. Paleo. 12, 38A.

Lehman, T.M., 1990. The ceratopsian subfamily Chasmosaurinae: sexual dimorphism and systematics. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 211–229.

Matthew, W.D., Brown, B., 1923. Preliminary notices of skeletons and skulls of deinodontidae from the Cretaceous of Alberta. Am. Mus. Nov. 89, 1–9.

Powell, J.S., 2000. Sexual dimorphism in archosaurs: a phylogenetic, morphological, and morphometric approach. Ph.D. Dissertation, George Washington University, Washington, DC.

Raath, M.A., 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 91–105.

Reese, A.M., 1915. The Alligator and its Allies. Knickerbocker, New York.

Romer, A.S., 1956. Osteology of the Reptiles. University of Chicago, Chicago.

Sato, T., Cheng, Y., Wu, X., Zelenitzky, D.K., Hsiao, Y., 2005. A pair of shelled eggs inside a female dinosaur. Science 308, 375.

Schweitzer, M.H., Wittmeyer, J.L., Horner, J.R., 2005. Gender-specific reproductive tissue in ratites and *Tyrannosaurus rex*. Science 308, 1456–1460.

Thulborn, R.A., 1974. A new heterodontosaurid dinosaur (Reptilia: Ornithischia) from the Upper Triassic red beds of Lesotho. Zool. J. Linn. Soc. Lond. 55, 151–175.

Wake, M.H., 2000. Integrative biology as a framework for education and training. Biol. Int. 39, 14–18.

Weishampel, D.B., Chapman, R.E., 1990. Morphometric study of *Plateosaurus* from Trossingen (Baden-Württemberg, Federal Republic of Germany). In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, Cambridge, pp. 43–51.

Witmer, L.M., 1994. The extant phylogenetic bracket and the importance of reconstructing the soft parts of fossils. In: Thomason, J.J. (Ed.), Functional Morphology in Vertebrate Paleontology. Cambridge University Press, Cambridge, pp. 9–33.