New data on tail lengths and variation along the caudal series in the non-avialian dinosaurs (#48148)

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New data on tail lengths and variation along the caudal series in the non-avialian dinosaurs

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The caudal vertebral series of non-avian dinosaurs varied considerably in terms of overall length, total number of vertebrae, gross form and function. A new dataset confirms that there is little or no consistent relationship between tail length and snout-sacrum length; consequently, attempts to estimate one from the other are likely to be very error-prone. Patterns of changes in centra lengths across the caudal series vary among non-avian dinosaurs. However, despite this variability, we show that some overarching patterns do emerge with a number of taxa showing (proximal to distal) a series of short centra, followed by a series of longer centra, with the remainder of the tail consisting of a long series of centra tapering in length. This pattern appears consistent with some functional constraints as the series of longer centra are coincident with the major attachments of femoral musculature. Notably, this arrangement is not present in early lineages and may have evolved independently in different dinosaurian groups, providing further support for the suggestion that the arrangement was of functional importance. Finally, we suggest that the methods developed here to separate out groups of similar units as part of a series may be widely applicable to assessments of entire vertebral series in a range of extinct and extant vertebrate taxa and, indeed, in any study of taxa exhibiting repeating units (for example, segmented invertebrates).

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Abstract

The caudal vertebral series of non-avian dinosaurs varied considerably in terms of overall length, total number of vertebrae, gross form and function. A new dataset confirms that there is little or no consistent relationship between tail length and snout-sacrum length; consequently, attempts to estimate one from the other are likely to be very error-prone. Patterns of changes in centra lengths across the caudal series vary among non-avian dinosaurs. However, despite this variability, we show that some overarching patterns do emerge with a number of taxa showing (proximal to distal) a series of short centra, followed by a series of longer centra, with the remainder of the tail consisting of a long series of centra tapering in length. This pattern appears consistent with some functional constraints as the series of longer centra are coincident with the major attachments of femoral musculature. Notably, this arrangement is not present in early lineages and may have evolved independently in different dinosaurian groups, providing further support for the suggestion that the arrangement was of functional importance. Finally, we suggest that the methods developed here to separate out groups of similar units as part of a series may be widely applicable to assessments of entire vertebral series in a range of extinct and extant vertebrate taxa and, indeed, in any study of taxa exhibiting repeating units (for example, segmented invertebrates).

Introduction

The caudal vertebral series of the non-avian dinosaurs (hereafter simply ‘dinosaurs’) served many roles. Dinosaur tails had a biomechanical function in locomotion (e.g. Hutchinson, Ng-Thow-Hing & Anderson, 2007; Persons & Currie, 2011a) and balance (e.g. Hutchinson & Gatesy, 2001; Libby et al. 2012)), and some were specialized for behavioural roles including inter- and intraspecific combat (e.g. Mallison, 2011; Arbour 2009) and signaling (e.g. Persons, Currie & Norell, 2014). However, despite this importance, investigations of the osteological caudal anatomy of dinosaurs have been generally limited.

A major issue is the incomplete nature of dinosaur tails. Very few have been identified that are truly complete (i.e. represented by every single caudal vertebra in the series), and those that are complete show considerable variation both inter- and intraspecifically (Hone, 2012).

This makes comparisons between taxa and generalisations across clades difficult and limits the confidence of any extrapolations.

Studies on dinosaur tails have often focused on tails as flexible structures (Pittman et al., 2013) to support major muscle groups, in particular the caudofemoralis which serves as a major driver in locomotion (Allen, Paxton & Hutchinson, 2009; Persons & Currie, 2011a). Previous work has argued that the caudofemoralis has substantially influenced the form of anterior caudal osteology, and adaptations suggested to be linked to the caudofemoralis include haemal spine depth, prominent chevron and vertebral sulci (Persons and Currie 2011a, b; Cau and Serventi 2017), and, most frequently, the ‘transition point’ of the lateral processes (Russell, 1972; Gatesy, 1990; Gatesy and Thomason, 1995; Persons and Currie 2011b). The ‘transition point’ is the region of the tail where the lateral processes end, and, by extension, where the caudofemoralis is inferred to have terminated. The association of a major and functionally distinct muscle set with one region of the tail suggests that dinosaur tails may have been modular, with different regions along the tail functioning in different ways. This is obviously true of dinosaurs that bear highly-derived caudal features, such as pygostyles or tail-clubs, but may also be true more generally, and such derived caudal features may also be associated with less apparent morphological diversity within other regions of the tail.

Here, we focus on a single aspect of the dinosaur caudal series: variation in anteroposterior centrum length. Little work has been previously done examining patterns of centrum lengths, although these have obvious influence on tail structure and by extension, may have influenced function. Assuming otherwise equivalent form, a series of long vertebrae would, as a unit, provide relative stiffness and stability to a tail (or at least parts of it), while series of shorter vertebrae would provide a zone of greater relative flexibility (e.g. see Persons, Currie & Norrell, 2014). Compared to the rest of the axial column, the caudal series of vertebrates is generally simplified. The number of vertebrae is correlated with body size in many basal vertebrates (Head & Polly, 2007), but less so in those taxa where there is regionalization and functional constraint (as in birds and mammals – Wake, 1979). The tail however may also vary considerably, even in mammals – both in terms of caudal count and total length (e.g. Garland, 1985; Cavallini, 1995) – suggesting it is relatively free of such constraints.

Such possible variation in role and morphology has yet to be explored. Indeed, changes in caudal centra have typically been considered simple reductions along the length of the tail. For example, Sereno (1997, p185) says of *Psittacosaurus* that "[t]he caudal centra show a regular decrease in length from the first to the last centrum" and Gilmore (1936) gives a similar description of the first 40 caudals of *Apatosaurus*. Although such statements may have been deliberately simplified assessments of the condition seen in the respective tails, they do not reflect the available data. *Apatosaurus* for example, shows sections of increase in the proximal vertebrae (in terms of both proportional and absolute centrum lengths) (Fig. 1). Similarly, in the tail of *Psittacosaurus*, although the vertebrae never increase in absolute length, the vertebral series shows sections of stability in length and decreases are not always regular (Sereno, 1997).

Wide variations in the bauplans of dinosaurs (body size, bipeds and quadrupeds etc.) and various derived condition (tail clubs, pygostyles) may also be associated with greater diversity within tails than currently appreciated. As such, the pattern of vertebra length in the tails of dinosaurs is an area in need of assessment, and we observe that at least some dinosaur tails shown considerable variation in the arrangements of the lengths of series of caudal centra.

In this context, we hypothesise that there is high variation in tail length across the Dinosauria making total length difficult to predict (following Hone, 2012), and we would expect that the structure of the tails of bipedal taxa differs from that of quadrupeds. We predict that centrum length does not follow a simple decrease in length in successive vertebrae and that the lateral processes are associated with a major change in tail function and therefore centrum lengths.

Institutional Abbreviations

AMNH American Museum of Natural History, New York; BMNS Belgium Museum of Natural Sciences, Brussels; CAGS Chinese Academy of Geological Sciences, Beijing; CM Carnegie Museum of Natural History, Pittsburgh; CMN Canadian Museum of Nature, Aylmer; CYGYB / CYNG Chaoyang Paleontological Museum, Chaoyang, Liaoning; FMNH Field Museum of Natural History, Chicago; GIN / Gi-SPS Institute of Geology, Mongolian Academy of Sciences, Ulan Baator; GMZ Grant Museum of Zoology, London; IGM Mongolian Academy of Sciences, Ulan Baator; IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; JME Jura Museum, Eichstätt; JMP Henan Geological Museum, Henan Province; LPM Liaoning Provincial Museum of Paleontology, Liaoning; MBR Museum für Naturkunde, Berlin; MNA Museum of Northern Arizona, Flagstaff; MPC Mongolian Paleontological Centre, Mongolian Academy of Sciences, Ulan Baator; NHM British Museum of Natural History, London; OMNH Oklahoma Museum of Natural History, Norman; PIN Paleontological Institute, Russian Academy of Sciences, Moscow; PMOL Paleontological Museum of Liaoning, Shenyang Normal University, Shenyang; QM Qijiang Dinosaur National Geological Park Museum, Liaoning; ROM Royal Ontario Museum, Toronto; RTMP Royal Tyrrell Museum of Palaeontology, Drumheller; SC Italian State Collections; SMA Sauriermuseum Aathal, Aathal; UCMP University of California Museum of Paleontology, Berkeley; USNM Smithsonian Museum of

Natural History, Washington, DC; YPM Yale Peabody Museum, New Haven; ZDM Zigong Dinosaur Museum, Zigong.

Materials & Methods

We expanded on the dataset of Hone (2012), with additional data collected from direct measurement of specimens, from measurements of photographs, and from the literature. We identified previously overlooked and new material ourselves and also through suggestions from various sources (see acknowledgements). It is possible that the inevitable variations and slight inconsistencies of collecting data from specimens vs the literature or photographs may affect narrow results. Therefore, we also took one specimen (a hadrosaur – TMP 1998.058.001) as a test case for variation in measurements between first hand observations and photographs. Each caudal centrum length was measured physically 10 times, and the same specimen was then photographed and another 10 replicate measurements obtained from these photographs. Segmented regressions were then fitted in the same way as the rest of the study, to both independently estimate the break points and in particular their congruence to each other, and to estimate the transition point (vertebra 12).

A complete tail was defined as one where every vertebrae was present down to the last caudal. The last caudal can typically be identified by a rounded posterior face and a lack of postzygopophyses and/or neural spine (Hone, 2012). Additional tails were regarded as complete where, although one or more elements were not preserved, the absent material could be accurately recorded because there was either an impression of the missing material in the matrix or the missing material was bounded by other elements. Incomplete tails were also included where it was felt that the missing material could be accurately reconstructed from other specimens of the same genus or species. For example, a total tail length was calculated and included where two or more individual specimens were complete enough to suggest the animals had very similar body sizes, and where the tails of both included a series of overlapping elements (e.g. an anterior tail portion and a posterior tail portion, with both possessing the last chevron or last lateral process pair). Total tail length was taken as the sum total of all caudal centra lengths (either as measured on a specimen or described in a paper, or measured as a single piece for those specimens where the centra were closely appressed together). In most cases the live animals would have possessed intervertebral discs that would have increased tail length, but these cannot be easily estimated and so were simply excluded.

Total femoral length was taken as a proxy for mass / body size (following Hone, 2012) for each specimen. Although other proxies (e.g. femur circumference) are stronger correlates of mass, femur length is appropriate for such datasets and the nature of many of the specimens (data collected from the literature, or compressed / crushed in preservation) means that length is often the only available measurement or the only one that can be obtained with any confidence. To examine the relationship between tail length and body size, we compared snout to sacrum length and tail length using a linear regression (see Hone, 2012). Since in some cases measurements came from different individuals, we scaled both against the femur of the specimen from which it was measured. This was also carried out for various subsets of the data to test the hypothesis that locomotion patterns of different groups would affect tail length. We therefore looked at four broad divisions of dinosaurs based on a general understanding of their locomotion: obligate bipeds (theropods, non-sauropodan sauropodomorphs), obligate quadrupeds (sauropods, thyrophoreans), bipeds and facultative bipeds (iguanodontids, hadrosaurs, psittacosaurids) together, and quadrupeds and facultative bipeds together.

In most cases, incomplete tails were not included in the analyses as it was considered impossible to ascertain the missing material based on the variations in caudal counts and the presence of both pygostyles and a lack of tapering in long series of caudals seen in some dinosaur tails (see below). Even tails that appear to be tapering consistently to a tip may have some considerable length still missing (as with e.g., *Diplodocus*). However, in an attempt to maximise the limited available data, we also sourced tails that were incomplete, but considered likely to be close to completeness. Such tails can at least be used to demonstrate minimum tail lengths, as an incomplete tail that is as long as or longer than a complete tail still demonstrates a genuine difference (data are provided in the Appendix).

The definition of what constitutes a 'nearly' complete tail is necessarily subjective given the limitations of the available information, but the intention was to include only those judged to have very few caudals missing and / or only a very short amount of the tail missing in terms of length. In order to estimate this, we took into account the degree of tapering of the tail, the length of material preserved and the length of the tail of close relatives. For example, not included is a specimen of the diplodocid sauropod *Barosaurus* (McIntosh, 2005) which has 29 preserved caudals that total over 6 m in length (against a femur of just 1.4 m in total length). However, the last caudal in this preserved series is some 171 mm long and, while some sauropods have as few as 35 caudals (Borsuk-Bialynicka 1977), a large amount of tail is considered likely missing in *Barosaurus*, given the size of the caudals present and the considerably higher number of caudals in other diplodocids (e.g. Gilmore, 1936). Note that the holotype of the small hadrosaur *Tethyshadros* (Dalla Vecchia, 2009) was incorrectly considered complete in Hone (2012) and so is not in the datasets.

The patterns of individual caudal centrum lengths that make up dinosaurian tails were also analysed. Here data from the above specimens was supplemented with additional but incomplete tails as the analysis looked at changes in individual centra as part of a series, rather than the tail as a whole unit. Note that even tails that can be diagnosed as complete are not always included in the analysis since either information on individual vertebrae lengths was not available in the literature, or the divisions between the vertebrae could not be reliably measured (e.g. the holotype of *Jinfengopteryx* – CAGS IG 040801).

To test the hypothesis that caudal centrum lengths do not follow a simple decrease in size along the series we used segmented regression (also known as piecewise or broken stick regression) to identify transitions in centrum length (break points). This was then compared with the boundary between the muscular and non-muscular parts of the tail (transition point). Essentially, this approach, where appropriate, fits a series of linear regressions to specific subsets of the data. For example, in *Apatosaurus* (CM 3378), the first section covers vertebrae 1–20, the second vertebrae 21-35, the third vertebrae 35-67 and the final section from vertebra 67-84 (Fig. 2). Clearly, however, in some cases a simple linear regression will provide a better fit to the data. To test this, a Davies test (Davies, 2002) was used to test for a non-constant regression parameter in the linear predictor (vertebra number) on centrum size using the R package segmented version 0.4-0.0 (Muggeo, 2003, 2008) implemented in R version 3.0.3 (R core team, 2014). In effect, this allows us to fit a segmented regression where the data support this (see for example *Apatosaurus* in Fig. 2) and a linear regression where there is no evidence to support a more complex fit (e.g., *Opistoceolocaudia* in Fig. 2).

Where the Davies test suggests that a segmented regression is appropriate, the next question is how many segments to fit. Candidate models with 1-4 breaks were fitted using *segmented* and the best model selected on the basis of the Akaike Information Criterion (Akaike, 1974). In essence, this approach selects the model which best balances explanatory power with simplicity. An upper limit of four breaks was chosen since some specimens had 20 or fewer vertebrae, limiting the number of breaks that could be plausibly fitted.

In this study, models used the default parameters in *segmented*, with quantiles as the starting points for the iterative breakpoint analysis, but with 50 bootstrap samples and a maximum of 10 iterations. Candidate models that could not be fitted in *segmented* (usually because of gaps in the data) were discarded.

Results

Tail length vs snout-sacrum length

The model suggests that tail length is an extremely poor predictor of snout to sacrum length (Fig. 3) (linear regression of snout/sacrum to femur ratio on tail to femur ratio: $F_{1,21} = 0.11$, $p = 0.74$). For example, *Scutellosaurus* has a tail to femur ratio of 8.8, and with a femur length of 82 mm, this corresponds to an estimated snout-sacrum size between 263.0 and 485.1 mm though the real value is much closer to the upper bound of 405 mm. At the opposite end of the scale, the tail to femur ratio of 1.2 in *Epidexipteryx* would correspond to an estimated snout-sacrum range of 173.4 to 259.1 mm although the actual value is outside of even this broad range at 158 mm.

If we attempt to minimise problems due to intraspecific (ontogenetic) scaling or phylogenetic bias and restrict the analysis to the largest individual of each species (where the full dataset contains more than one individual), and when juveniles or indeterminate taxa are removed the same pattern is retained (linear regression: $F_{1,16} = 0.01$, $p = 0.91$). This is also true of the various subdivisions by locomotor style: bipeds alone (linear regression of snout-sacrum:

femur on tail to femur): F(1,8)=0.01, p =0.92; quadrupeds alone: F(1,5)=0.2938, p=0.61; bipeds plus facultative bipeds: F(1,14)=0.331, p=0.57; quadrupeds plus facultative bipeds: F(1,11)=0.009, p=0.92. In short, tail size is not clearly related to body size in non-avian dinosaurs, even allowing for broad distinctions in locomotor style.

Patterns of caudal vertebrae length

Across the Dinosauria, most tail sequences passed the Davies test and so could be reconstructed with one or more breaks to the series of individual centrum lengths. There was at least some consistency in the results within clades, with several specimens of single taxa showing similar patterns to one another (e.g. *Archaeopteryx* – Fig. 4) though others were inconsistent (e.g. *Coelophysis* – Fig. 5).

Break points

For 18 out of 25 specimens, the distance between the break point and transition point was lower than would be expected by chance (exact binomial test, p=0.043) (Fig. 6). Where multiple measurements were taken from one hadrosaur tail as a test of consistency of measurements, the congruence between break points as produced from direct measurements of the specimen and those taken from a photograph, was good. In both cases, the model fitted four break points (specimen (mean±se): 12.0±1.59, 45.8±3.48, 61.5±3.90, 74.7±0.71; photographs 11.9±1.99, 48.5±1.29, 57.3±1.07, 59.4±1.04). In particular, both methods fitted a break point very close to the actual transition point, and even at the distal end, where there was slight disagreement, all four of the break points fitted from photographs were encompassed with the standard errors of break points derived from the specimen itself (Fig. 7). This suggests that the data taken from photographs for various specimens will yield accurate data.

Discussion

Overall lengths of dinosaurian tails

Our hypothesis that there is high variation in tail lengths across the dinosaurs, and that tail lengths do not correlate well with body size (i.e. snout-sacrum length) was supported with very wide confidence limits for predictions of one based on the other (Fig.3). However, the prediction that there would be similarities between bipedal or quadrupedal taxa was not met. Even when considering facultatively bipedal or quadrupedal taxa with obligate biped and quadrupeds, no clear relationship between body size and tail length was recovered.

The data from the ‘near complete’ tails is of course limited in its use given these issues, though at least some of the specimens recorded here do suggest that there may be some consistency within groups. Additional data may alter this pattern and suggest a greater level of consistency, but for most dinosaur groups, attempting to estimate the total length of a tail from anything other than a near complete series is subject to a wide range of error and uncertainty, as seen even within some small clades (e.g., Scansoriopterygidae). Dinosaur tails were also likely evolutionally plastic and frequently assumed forms to serve specific functions (or specific combinations of functions) adding further to interspecific, and perhaps also intraspecific, variation.

Caudal length patterns in dinosaur tails

Considerable variation is seen not just in the overall and proportional sizes of dinosaur tails but also in the lengths of the individual caudal centra that comprise them. Although the distalmost caudals of a series are generally smaller than more proximal ones, over a short section of consecutive elements there may be patterns of increasing length, stability, or decreasing length (and all three may occur in one individual e.g., *Apatosaurus* CM 563 – Gilmore, 1936). Although the datasets here are somewhat limited, they do cover a wide range of dinosaurian biology – large and small, herbivores and carnivores, bipeds and quadrupeds, long and short tails, and taxa from the Late Triassic to the end of the Cretaceous. Thus some considerable variation may be expected, but even so there are some clear patterns. Most notably, many dinosaurs show repeated series of, on average, increasing and decreasing centra lengths along the caudal series as demonstrated by the positions of break points and the associated regressions.

Most taxa show an early short series of tail vertebrae decreasing in length sequentially, then a short series increasing in length (typically including the longest centra in the tail), followed by a long series of progressive decrease. These include at least one specimen each of *Kentrosaurus* (Fig. 8), *Leptoceratops, Centrosaurus* (both Fig. 9)*, Lufengosaurus* (Fig. 10)*, Apatosaurus*, *Camarasaurus* (both Fig. 2), *Gorgosaurus, Tyrannosaurus* (both Fig. 11), *Ornithomimus, Nomingia* (both Fig. 12), *Microraptor,* and *Velociraptor* (both Fig. 13). Note that frequently the first and second caudal vertebrae may vary from this overarching pattern. While not universal, this pattern is widespread in the Dinosauria. Other specimens are not so far from this pattern (e.g., *Dilophosaurus* (Fig. 11), *Ingenia* (Fig. 12)*, Ouranosaurus* (Fig. 14)*, Lambeosaurus* (Fig. 15)). It may be that this pattern is even more prevalent but is, in some instances, hidden from the tests used here by some variation or lack of data. For example, the proximal caudals of *Diplodocus* and *Majungasaurus* are not recorded, and although those preserved do seem to conform to the pattern, it cannot be confirmed.

Other taxa do deviate considerably from the short-long-shortening pattern described above (e.g. *Plateosaurus* (Fig. 9)*, Juravenator* (Fig. 11)), indeed the caudals of *Coelophysis* tend to increase in length for much of the series (Fig. 5). Various constraints may confound the basic pattern and affect the overall distribution. For example, the majority of the vertebrae in the dromaeosaurs *Velociraptor*, *Deinonychus* and *Microraptor* are bound by a complex series of extended zygopophyses and chevrons that stiffen the tail and perhaps free the vertebrae from normal functional constraints. This may explain some of the variation seen between specimens and genera (Fig. 13). However, the patterns of centrum lengths seen in the tails of all three specimens of *Archaeopteryx* and the putative glider *Microraptor* are strikingly similar and, although only a very limited set of data, do show a level of consistency not seen in other groups (Figs. 4, 13). This suggests at least the possibility that this similarity in form is connected to the shared tail function of control in flight. It has been noted by Gatesy and Dial (1996) that *Archaeopteryx* would benefit in flight control from a stiff tail that was only flexible at the very base and this is reflected here with a proximal section of short centra and then a very rapid jump to considerably longer centra.

In contrast, *Juravenator* is very different to most other taxa (Fig. 12), though this is perhaps the result of the holotype specimen being a juvenile. However, Chiappe and Göhlich (2010) noted that part the caudal length pattern of *Juravenator* (with a stable series then a series of short centra, then long, and then shorter again) may be consistent across at least some compsognathids. This suggest that *Juravenator* is perhaps not just an outlier on its own, but is representative of a pattern that is normal for the clade. Still, it remains unusual compared to most other dinosaurs.

Error

Given the limited availability of data and the problems associated with sourcing information from the literature, mounted specimens, or those with poor preservation, there is likely to be some error in the data. Distortion, if systematic within a specimen, would still preserve the pattern overall and if random (within or between specimens) should have no overall effect. This is similar to any issues of measurements taken from the literature where different authors may have used slightly different metrics to take the length of the caudal centra, but we would expect consistency within specimens and thus preservation of patterns. As noted above, our own formal assessment of the possible differences between the measurements from a specimen and from a photograph produced similar results, especially for the prediction of the transition point which was identical in both and correctly identified as caudal vertebra 12 (Fig. 7).

The vertebrae of smaller specimens may cause problems as these will be harder to measure with equivalent accurately. For example, the long sequence of identical values seen in *Juravenator* could be because the animal is still a juvenile or may genuinely reflect the unusual caudal anatomy of this genus (or of compsognathids as a whole). However, it could simply be because the vertebrae are so small that variation between them (even when measuring to the nearest 0.1 mm) was difficult to detect (as also perhaps seen in specimens of *Psittacosaurus*). Similarly, the alternating sequence of long-short-long seen in various specimens of *Apatosaurus* as described above, may simply be size related (it is easier to measure long vertebrae and find clear differences between them). However, these errors in measurements are collectively likely to be unbiased overall and so should not affect the results or general patterns reported here.

There is some consistency within clades, with for example two specimens of *Leptoceratops* (despite differing caudal counts – Fig. 9), three specimens of *Archaeopteryx* (Fig. 4), and two tyrannosaurids (Fig. 11) all showing similar patterns to one another, suggesting consistency in the data and the analysis. Two specimens of *Velociraptor* are very similar, although a third is rather different, but similar to its near relative *Deinonychus* (Fig. 13).

Implications

Assuming equivalency of vertebral articulation, for a given unit of length of tail, more joints will increase flexibility and fewer joints will make it less flexible. Thus, shorter centra imply greater zonal flexibility and longer ones, greater zonal stiffness. As such, we can use the varying lengths of centra within different parts of dinosaur tails to infer differing levels of flexion.

The repeated pattern seen here of a series of short centra, then a series on long ones, and then finally a series of tapering caudals suggests that many dinosaurs had a flexible tail base, then a stiffened section and finally a more flexible section. Our hypothesis that the transition point (i.e. the termination of the attachment of the caudofemoralis musculature) is linked to a major change in tail function (as implied by centrum length) is borne out by our analyses. We recorded the last centrum to preserve a lateral process from specimens directly or where they were recorded in the literature. Comparing these to the data on serial variation shows that the transition point often coincides closely with a shift in pattern of centra length, (Fig.6) as determined by the changes in regression lines (e.g. *Lambeosaurus* (Fig. 15)*, Juravenator, Gorgosaurus, Tyrannosaurus* (all Fig. 11)*, Ornithomimus* (Fig. 12)).

Even in taxa where this pattern does not hold, there is still some evidence that the transition has an influence on caudal length, as the point recorded may be associated with a slight ‘hump’ in the data (i.e. a short increase and then decrease in vertebral length over just four or five vertebrae) as seen in e.g. *Plateosaurus* (Fig. 10) and *Nomingia* (Fig. 12). As the transition point is perhaps better thought of as a ‘zone’ (Persons & Currie 2011b), a little leeway must be allowed and we would not expect a perfect correlation between the change in centrum length and the last vertebra supporting a lateral process. Even so, it is clear that the calculated break points in the series do often fall exactly or within one or two vertebrae of the last centrum with a lateral process. Based on this discovery, it may be possible to deduce the transition point in some specimens even if the lateral processes and chevrons are missing or damaged based on the pattern of the lengths of centra. The series of long vertebra that correspond to most of the length of the anterior tail up to the transition point would make the tail relatively stiff. This would improve the efficiency of the caudofemoralis muscles as this stiffness would reduce energy loss though movements between vertebrae and ensure that most effort of contract led to driving the femur and not flexing the tail.

Posterior to the transition point, the requirement for great stiffness is presumably relaxed and thus lead to the simple pattern of general reduction in size of successive centra moving posteriorly. Simple selection for reduction in mass distally (with obvious exceptions such as taxa bearing tail clubs) would lead to the pattern seen here and may be the typical primitive condition for reptilian tails (see the data for *Varanus* and *Crocodylus* – Fig. 16, though clearly this is a very limited dataset).

These two more posterior sections of the tail thus have simple mechanical explanations, but this does not explain the series of short centra at the base of the tail. We suggest that this section would allow the entire tail to flex as a unit, as clearly any proximal motion of the tail would also affect any more distal portion of the tail. Thus a flexible section at the very base of the tail allows the entire tail to be moved without compromising the stiffness of the successive section. This is therefore likely a trade-off between flexion and stiffness. It should also be noted that the very proximal section of the tail may also have been less strongly influenced by contractions of the caudofemoral musculature, because the most proximal caudal vertebrae typically lack chevrons. This would afford far less muscle attachment than in the immediately posterior section of the tail.

Evolution of dinosaurian caudal centra series

This short-long-decreasing pattern was likely acquired independently in multiple lineages of dinosaurs. A number of Triassic and / or basal forms (*Coelophysis*, Fig. 5; *Plateosaurus*, Fig. 10)*,* lack the pattern and retained the apparently primitive diapsid / archosaur condition of a simple progressive decrease along the length of the tail. The repeated evolution of various osteological structures able to passively stiffen the tail (e.g. elongate zygopophyses and chevrons in some theropods, hyposphene-hypantra articulations in some sauropods, ossified tendons in ornithischians) suggests that tail rigidity was favoured repeatedly in various groups of the Theropoda, Sauropoda and Ornithischia. Thus, the apparent distribution of the short-long-decreasing pattern seen here in later theropods, sauropods and ornithischians may have also arisen independently from similar selective pressures favouring a small zone of high flexibility immediately posterior to the hips and an extended zone of stiffness that helped improve locomotory efficiency.

Despite the wide variations in patterns of elongation and constriction in centrum lengths, it is clear that in at least some cases where there is a reasonable number of caudals preserved and their positions known, it may be possible to reconstruct the missing ones with some confidence. Repeated patterns within and between taxa, and long strings of caudals with a consistent pattern of elongation or reduction means that the sizes of missing vertebrae may be estimated. Potentially even the total length of a tail may be estimated if much of the series is preserved. However, in general this is likely to be difficult – the variation seen here in the patterns of increases and decreases, and the differing numbers of vertebrae in those various sets of increases and decreases are highly variable and difficult to predict. In particular, the end of the tail is difficult to assess. While clearly any regression of caudal size that was decreasing successively would eventually suggest a centrum of near zero or negative length, at what point before this the tail would actually terminate cannot be estimated. Gilmore (1936) notes with relation to the 'whiplash' segment of the distal tail of *Apatosaurus* that "the uniformity in size of these terminal rod-like caudals is such that any loss would be difficult to detect" and similarly, this general problem of tail termination is further exacerbated by the presence of a pygostyle in some maniraptoran theropods.

The variation in caudal counts in taxa also has implications for other aspects of research. For example, taphonomic analyses may consider sorting or loss of elements by size and therefore knowing how many vertebrae and of what size ranges a given taxon has may be important. In an analysis of a bone bed dominated by the hadrosaur *Amurosaurus*, Lauters et al. (2008) looked at the different numbers of element types preserved. They suggested that the vertebrae of *Amurosaurus* were underrepresented in the bonebeds based on the estimated number of vertebrae in the axial column. However, with very little articulation known for remains of *Amurosaurus*, it cannot be easily estimated how long the tail was or how many caudals it possessed, with tails for hadrosaurs known to have as few as around 50 caudals (Horner, Weishampel & Forster, 2004) to over 75 (Lull & Wright, 1942). (There is of course also likely variation within the number of the cervical, dorsal and sacral series, though based on Hone [2012], this is likely to be much less of an issue than the caudal series). The results of Lauters et al. (2008) were robust and in this case such an issue is not likely to have had a major effect on their results, but the uncertainty surrounding the number of vertebrae in the axial column means that care should be taken when performing such an analysis. We suggest that, unless the true axial count is known with confidence, either caudals should not be counted, or upper and lower estimates of the number of vertebrae in the column should be employed, or such considerations should be limited to the lateral process bearing caudals (where the number is more certain).

Conclusions

Total tail length remains difficult to estimate for incomplete tails in the Dinosauria, and there is some strong variation both between and within family-rank equivalent clades for various taxa. However, there is some consistency in patterns of overall caudal lengths. Notably, the proximal part of the tail often consists of relatively short vertebrae, followed by a series of longer vertebrae and then a shift to decreasing centrum lengths beyond the transition point.

Although here used to investigate dinosaur tails, these methods have a much wider applicability in terms of investigating patterns across series of vertebrae or other sequential elements (e.g. rib length, scale size in reptiles, segment length in invertebrates etc.).

Acknowledgements

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Figure captions

Figure 1. A complete caudal series for the tyrannosaurid *Gorgosaurus* (RTMP 91.36.500). One of very few complete series that is also both articulated and preserved in three dimensions. Scale bar is 200 mm.

Figure 2. Regressions for centrum lengths within the tails of members of Sauropoda. Here, and for subsequent figures, predicted break points and their error bars are indicated at the bottom of each graph where these have been calculated, and the transition point (where known) is indicated by an arrow (the same point is inferred for both specimens of *Apatosaurus*). Both specimens of *Apatosaurus* are from the CM.

Figure 3. Relative size of snout to sacrum against relative tail length. Snout to sacrum vs tail length, with both measurements scaled to femur size (see Methods). Comparisons drawn from the same individual are shown as black circles; those from different individuals as open circles. The solid line shows the fitted (non-significant) regression; dashed lines show 95% confidence intervals for this regression. The grey lines show the range and distribution of tail to femur ratio for all of the species in our analysis. See also Table 1.

Figure 4. Regressions for centrum lengths within the tails for specimens of *Archaeopteryx*. The different specimens can be identified by their museum prefixes.

Figure 5. Regressions for centrum lengths within the tails for specimens of *Coelophysis*. The same transition point is inferred for all specimens. All three specimens are from the AMNH.

Figure 6. Mean distance between break point and transition point in 1000 randomisations, plotted against the actual distance. The grey line shows the 1:1 line; red lines show standard errors. For all but seven of the specimens, the actual distance was lower than the randomised distance (Exact binomial test, p=0.04).

Figure 7. Segmented regressions for specimen TMP1998.058.001. Segments derived from photographs (red) and from the specimen itself (blue). Both methods fitted a break point very close to the actual transition point, and with the exception of a break point right at the distal end, break points derived from one method overlapped with break points derived from the other.

Figure 8. Regressions for centrum lengths within the tails for members of the Thyrophorea. The stegosaur *Kentrosaurus* above, and ankylosaur *Dyoplocephalus* below.

Figure 9. Regressions for centrum lengths within the tails for members of the Ceratopsidae. The first two specimens of *Psittacosaurus* are from the AMNH and the two specimens of *Leptoceratops* are from the CMN.

Figure 10. Regressions for centrum lengths within the tails for non-sauropodan members of the Sauropodomorpha. Patterns of centrum lengths for a Jurassic and Triassic saruopodomorph.

Figure 11. Regressions for centrum lengths within the tails for members of the Theropoda. Centrum length patterns for non-maniraptoran theropods.

Figure 12. Regressions for centrum lengths within the tails for members selected non-paravain Maniraptora.

Figure 13. Regressions for centrum lengths within the tails for members of the Dromaeosauridae. The different specimens of *Velociraptor* can be identified by their museum prefixes.

Figure 14. Regressions for centrum lengths within the tails for members selected non-hadrosauroid Iguanodontia.

Figure 15. Regressions for centrum lengths within the tails for members selected Hadrosauridae.

Figure 16. Regressions for centrum lengths within the tails for two non-dinosaurian Reptiles – *Crocodylus niloticus* and *Varanus nilitocus*.

Table 1. Estimated ratio of body length (snout-to-sacrum) to tail length, with both scaled to femur size, with upper and lower 95% confidence intervals (cf. Figure 3). Also shown are the smallest and largest snout-sacrum sizes compatible with these confidence limits.

Genus	fit	lwr	upr	snout to sacrum (min)	snout to sacrum (max)
Dryosaurus	4.34	3.91	4.77	1290.6	1575.1
Othneilosaurus	4.38	3.93	4.84	1041.1	1282.5
Jeholosaurus	4.39	3.92	4.85	356.9	441.8
Leaellynasaura	4.71	2.43	6.99	170.3	489.6
Stegosaurus	4.29	3.70	4.88	2814.9	3707.8
Scutellosaurus	4.56	3.21	5.92	263.0	485.1
Scleidosaurus	4.40	3.90	4.91	1382.9	1741.9
Pinacosaurus	4.41	3.87	4.96	1546.6	1982.7
Dyoplosaurus	4.33	3.86	4.79	2169.3	2692.1
Saichania	4.37	3.94	4.80	1497.4	1823.0
Edmontosaurus	4.35	3.92	4.77	3841.6	4676.9
Lambeosaurus	4.32	3.84	4.80	4151.3	5181.7
Corythosaurus	4.33	3.86	4.79	4149.4	5149.5

Hadrosauridae_indet	4.35	3.92	4.77	2058.0	2505.5
Tenontosaurus	4.42	3.84	5.01	1802.8	2353.3
Parksosaurus	4.37	3.94	4.80	1024.4	1248.8
Psittacosaurus	4.31	3.79	4.83	594.9	757.9
Psittacosaurus	4.34	3.91	4.77	406.9	496.4
Psittacosaurus	4.33	3.89	4.78	252.9	310.6
Psittacosaurus	4.35	3.93	4.77	530.2	644.4
Archaeoceratops	4.26	3.51	5.01	680.3	971.6
Leptoceratops	4.33	3.86	4.79	1024.1	1268.9
Leptoceratops	4.30	3.74	4.86	860.5	1116.7
Leptoceratops	4.29	3.69	4.88	1075.2	1421.4
Protoceratops	4.31	3.79	4.83	98.5	125.5
Protoceratops	4.29	3.68	4.89	103.1	137.0
Centrosaurus	4.31	3.79	4.83	2803.9	3572.2
Anchiceratops	4.27	3.58	4.96	2651.9	3667.8
Lufengosaurus	4.37	3.94	4.80	2186.7	2665.7
Camarasaurus	4.36	3.94	4.79	2237.9	2718.6
Opisthocoelicaudia	4.33	3.87	4.78	5405.2	6673.4
Spinophorosaurus	4.41	3.87	4.94	4706.9	6007.3
Coelophysis	4.42	3.82	5.03	573.6	753.8
Gorgosaurus	4.37	3.94	4.80	2541.3	3098.0
Ornithomimid	4.33	3.89	4.78	1809.8	2221.5
Gallimimus	4.34	3.91	4.77	2600.8	3174.0
Ornithomimus	4.37	3.94	4.79	1670.9	2032.6
Sinocalliopteryx	4.41	3.87	4.95	917.9	1172.3
Caudipteryx	4.24	3.43	5.06	510.6	754.3
Caudipteryx	4.25	3.43	5.06	634.5	936.2
Nomingia	4.27	3.58	4.96	1021.4	1412.6
Mei	4.35	3.93	4.78	318.6	386.9
Jinfengopteryx	4.35	3.92	4.77	313.6	381.8
Anchiornis	4.45	3.71	5.20	NA	NA
Sinusonasus	4.34	3.90	4.78	522.0	640.0
Microraptor	4.39	3.92	4.85	NA	NA
Microraptor	4.33	3.87	4.79	379.3	469.0
Microraptor	4.44	3.75	5.13	322.9	441.3
Microraptor	4.42	3.84	5.00	199.8	259.9
Epidexipteryx	4.24	3.40	5.08	173.4	259.1
Eosinopteryx	4.32	3.82	4.81	153.0	192.3
Aurornis	4.34	3.91	4.77	254.0	310.3

Archaeopteryx	4.35	3.93	4.77	145.4	176.7
Archaeopteryx	4.33	3.87	4.79	214.1	264.6
Changyuraptor	4.34	3.91	4.77	629.2	768.5

APPENDICES:

Table 1. Master dataset of all data – Complete tail lengths, Snout-Sacrum lengths, Incomplete tail lengths, Centrum lengths, Transverse Processes, References.

SI Fig 1. Break points for ornithischian tails. Aligned caudal centra (black squares, spaces indicate missing vertebrae), break points as calculated (red points with error bars) and transition point (where known, blue triangles) for all ornithischians in the study.

SI Fig 2. Break points for sauropodomorph tails. Aligned caudal centra, break points as calculated and transition point (where known) for all sauropodomorphs in the study.

SI Fig 3. Break points for theropod tails. Aligned caudal centra, break points as calculated and transition point (where known) for all theropods in the study.

Figure 1

A complete caudal series for the tyrannosaurid *Gorgosaurus* (RTMP 91.36.500).

One of very few complete series that is also both articulated and preserved in three dimensions. Scale bar is 200 mm.

Figure 2

Regressions for centrum lengths within the tails of members of Sauropoda.

Here, and for subsequent figures, predicted break points and their error bars are indicated at the bottom of each graph where these have been calculated, and the transition point (where known) is indicated by an arrow (the same point is inferred for both specimens of *Apatosaurus*). Both specimens of *Apatosaurus* are from the CM.

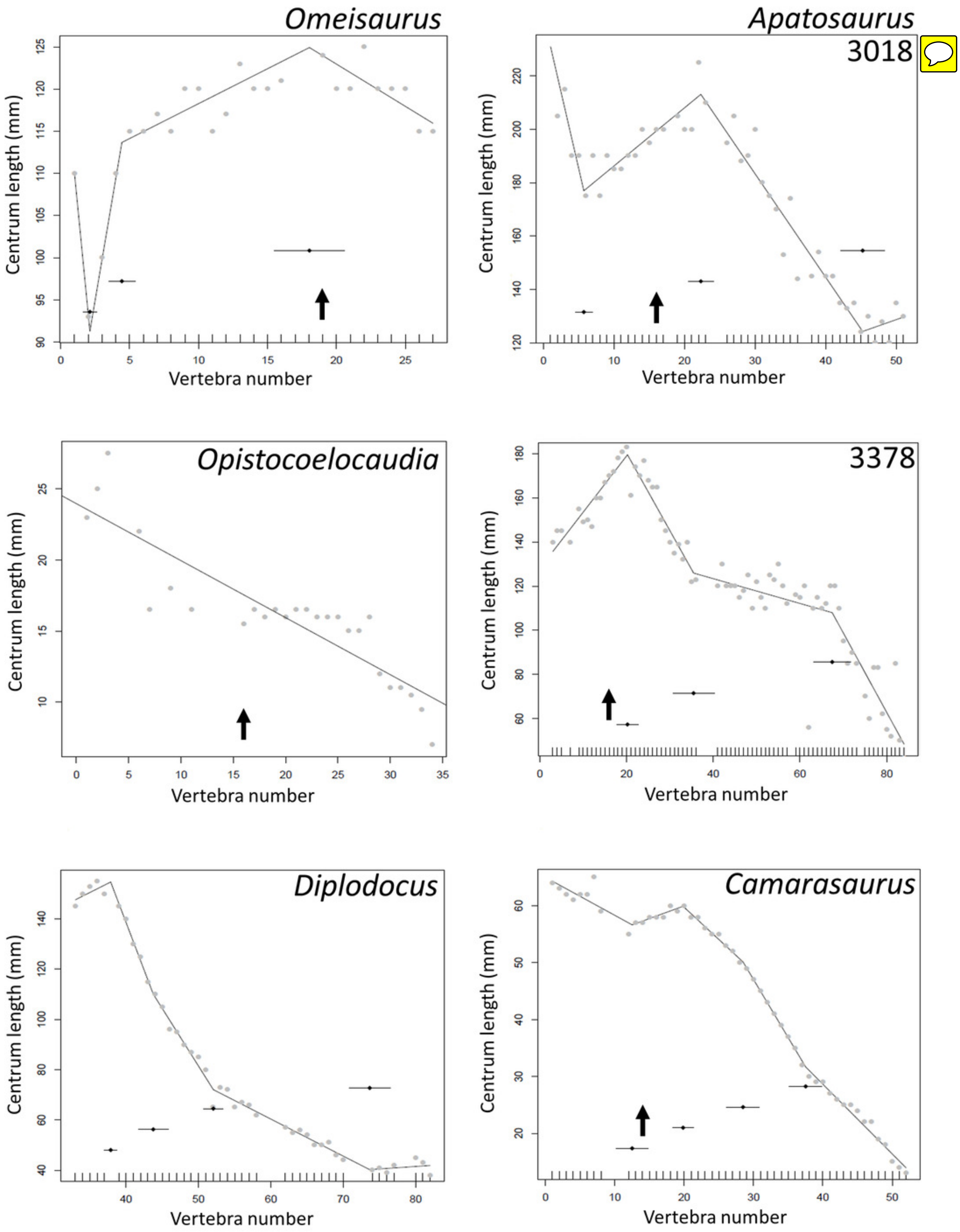

Omeisaurus
Centrum length (mm)
90
95
100
105
110
115
120
125
0
5
10
15
20
25
Vertebra number
Apatosaurus
3018
Centrum length (mm)
120
140
160
180
200
220
0
10
20
30
40
50
Vertebra number
Opistocoelocaudia
Centrum length (mm)
10
15
20
25
0
5
10
15
20
25
30
35
Vertebra number
3378
Centrum length (mm)
60
80
100
120
140
160
180
0
20
40
60
80
Vertebra number
Diplodocus
Centrum length (mm)
40
60
80
100
120
140
40
50
60
70
80
Vertebra number
Camarasaurus
Centrum length (mm)
20
30
40
50
60
0
10
20
30
40
50
Vertebra number

Figure 3

Relative size of snout to sacrum against relative tail length.

Snout to sacrum vs tail length, with both measurements scaled to femur size (see Methods). Comparisons drawn from the same individual are shown as black circles; those from different individuals as open circles. The solid line shows the fitted (non-significant) regression; dashed lines show 95% confidence intervals for this regression. The grey lines show the range and distribution of tail to femur ratio for all of the species in our analysis. See also Table 1.

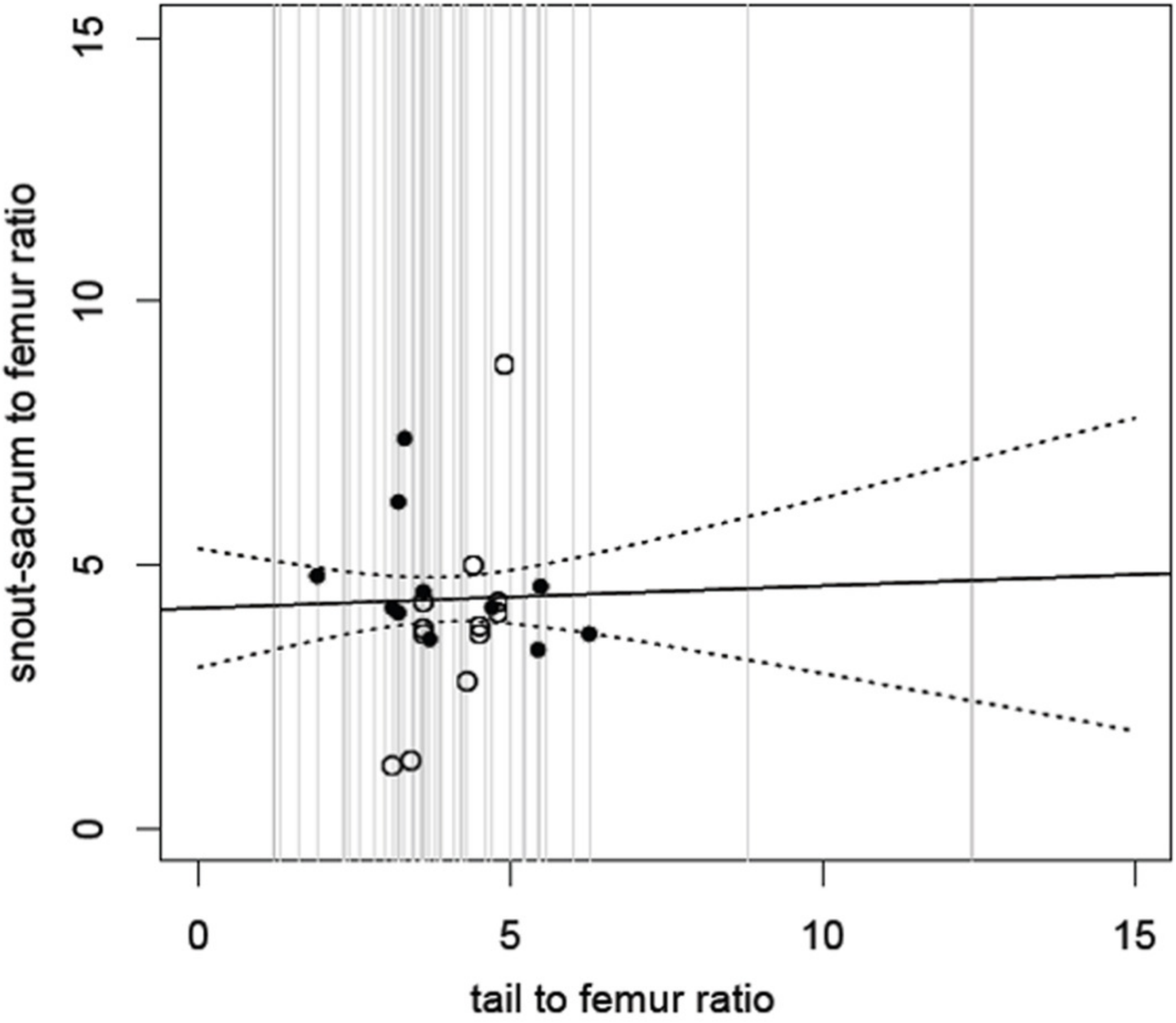

15
10
5
0
snout-sacrum to femur ratio
0
5
10
15
tail to femur ratio

Figure 4

Regressions for centrum lengths within the tails for specimens of *Archaeopteryx*.

The different specimens can be identified by their museum prefixes.

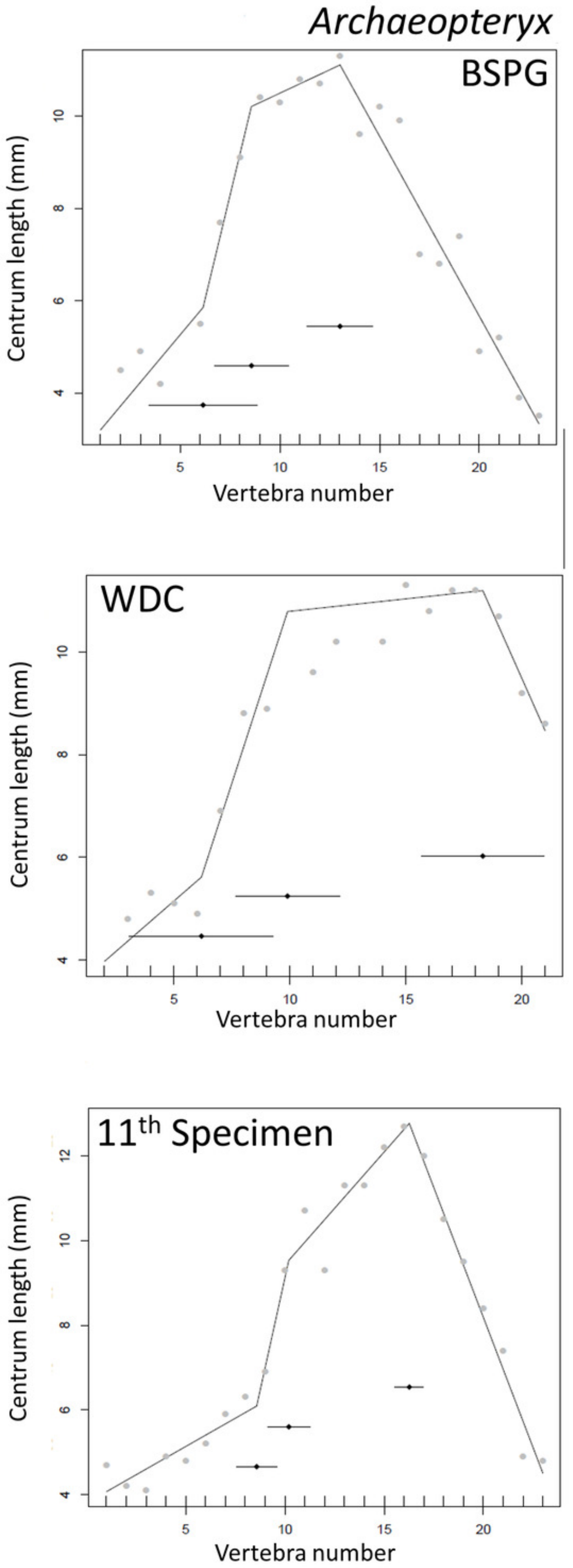

Archaeopteryx
BSPG
Centrum length (mm)
4
6
8
10
5
10
15
20
Vertebra number
WDC
Centrum length (mm)
4
6
8
10
5
10
15
20
Vertebra number
11th Specimen
Centrum length (mm)
4
6
8
10
12
5
10
15
20
Vertebra number

Figure 5

Regressions for centrum lengths within the tails for specimens of *Coelophysis*.

The same transition point is inferred for all specimens. All three specimens are from the AMNH.

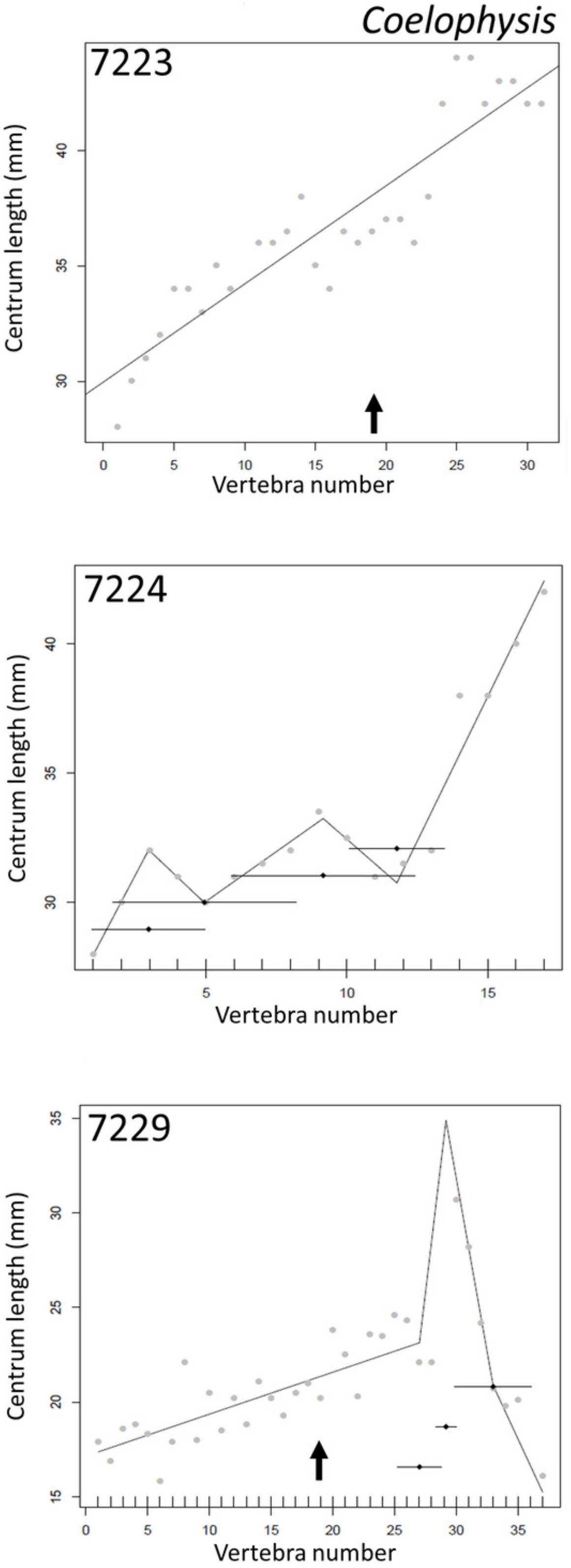

Coelophysis
7223
Centrum length (mm)
30
35
40
0
5
10
15
20
25
30
Vertebra number
7224
Centrum length (mm)
30
35
40
5
10
15
Vertebra number
7229
Centrum length (mm)
15
20
25
30
35
0
5
10
15
20
25
30
35
Vertebra number

Figure 6

Mean distance between break point and transition point in 1000 randomisations, plotted against the actual distance.

The grey line shows the 1:1 line; red lines show standard errors. For all but seven of the specimens, the actual distance was lower than the randomised distance (Exact binomial test, p=0.04).

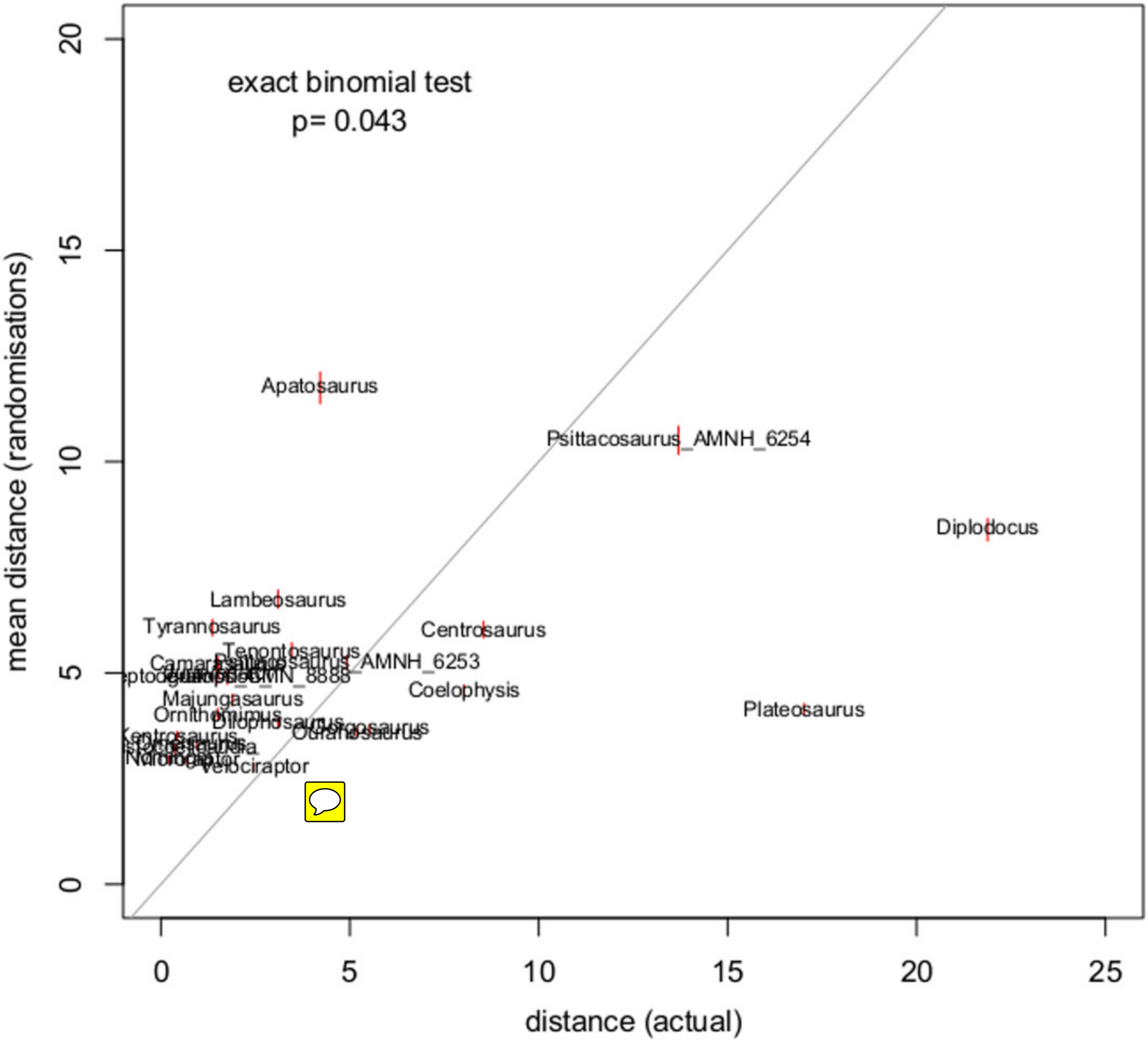

exact binomial test
p= 0.043
mean distance (randomisations)
distance (actual)
0
5
10
15
20
25
Apatosaurus
Psittacosaurus_AMNH_6254
Diplodocus
Lambeosaurus
Tyrannosaurus
Centrosaurus
Tenontosaurus
Psittacosaurus_AMNH_6253
Camarasaurus
Coelophysis
Plateosaurus
Majungasaurus
Ornithomimus
Dilophosaurus
Ouranosaurus
Kentrosaurus
Velociraptor

Figure 7

Segmented regressions for specimen TMP1998.058.001

Segments derived from photographs (red) and from the specimen itself (blue). Both methods fitted a break point very close to the actual transition point, and with the exception of a break point right at the distal end, break points derived from one method overlapped with break points derived from the other.

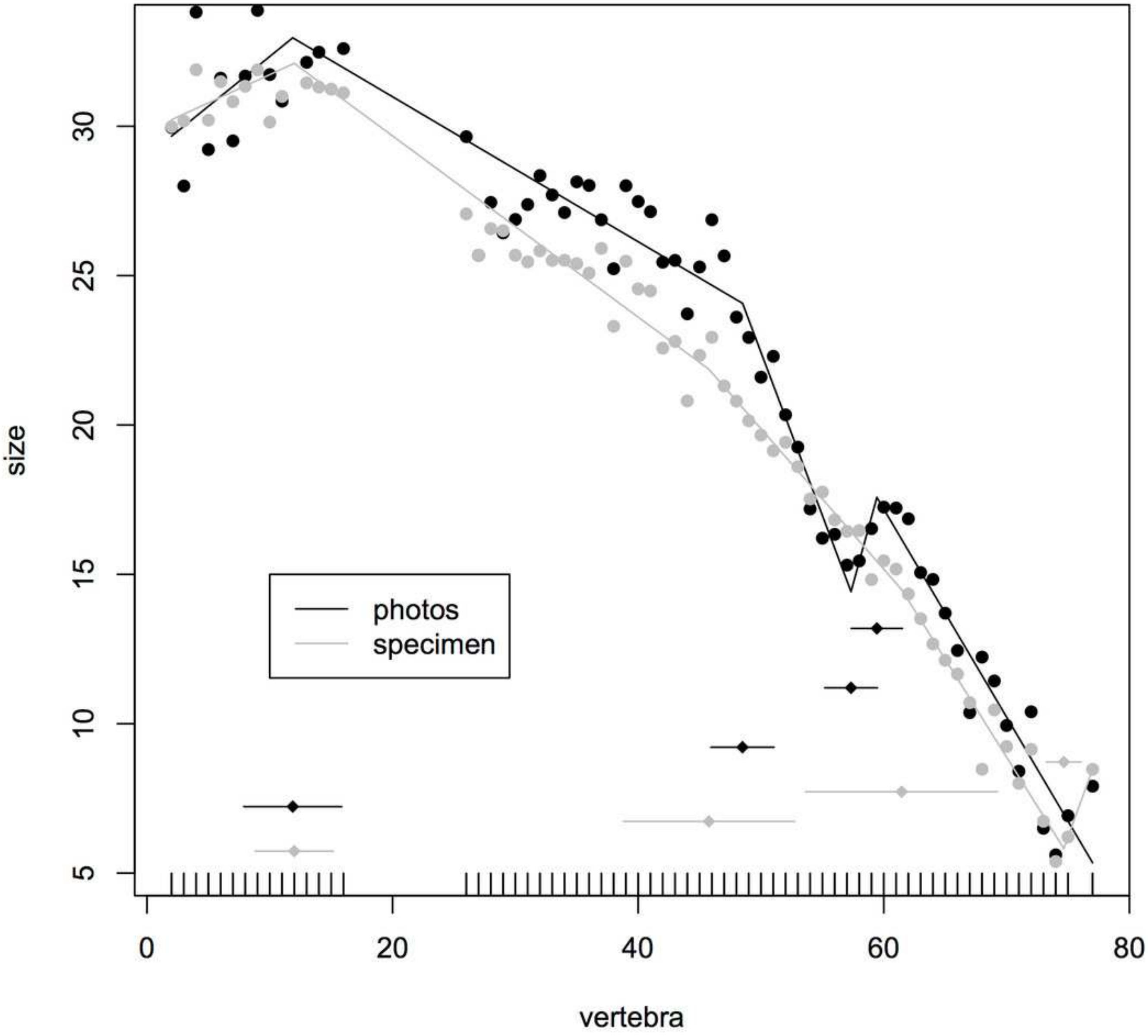
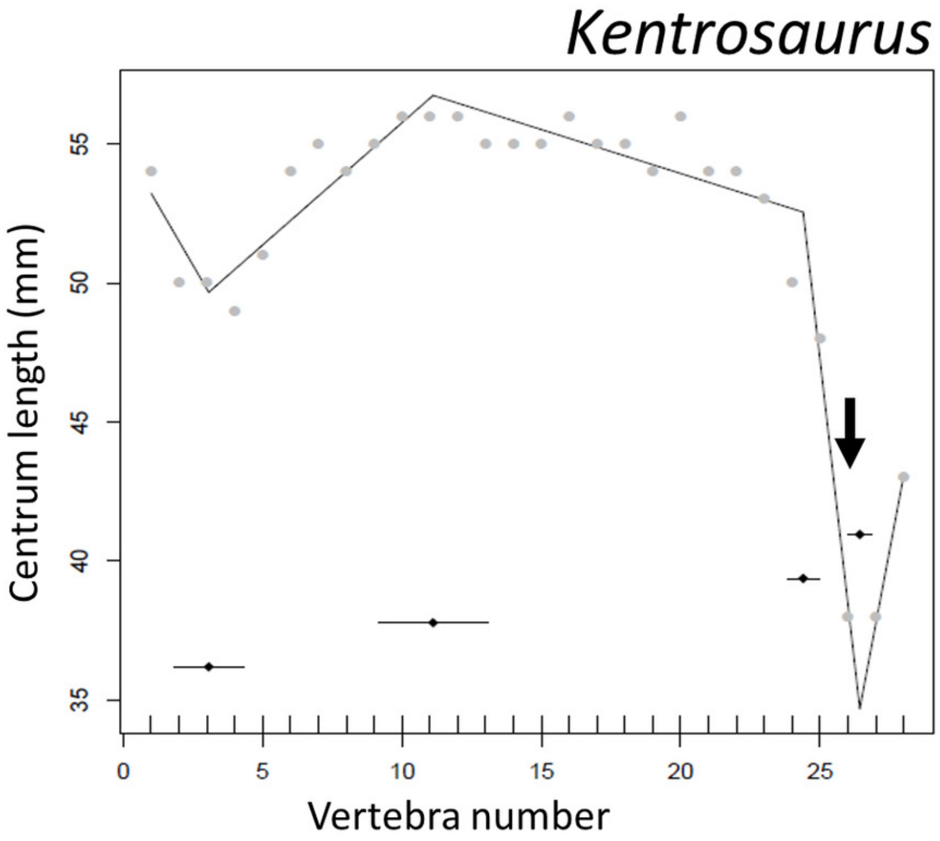

size
30
25
20
15
10
5
0
20
40
60
80
vertebra
photos
specimen

Figure 8

Regressions for centrum lengths within the tails for members of the Thyrophorea.

The stegosaur Kentrosaurus above, and ankylosaur Dyoplocephalus below.


Kentrosaurus
Centrum length (mm)
35
40
45
50
55
0
5
10
15
20
25
Vertebra number

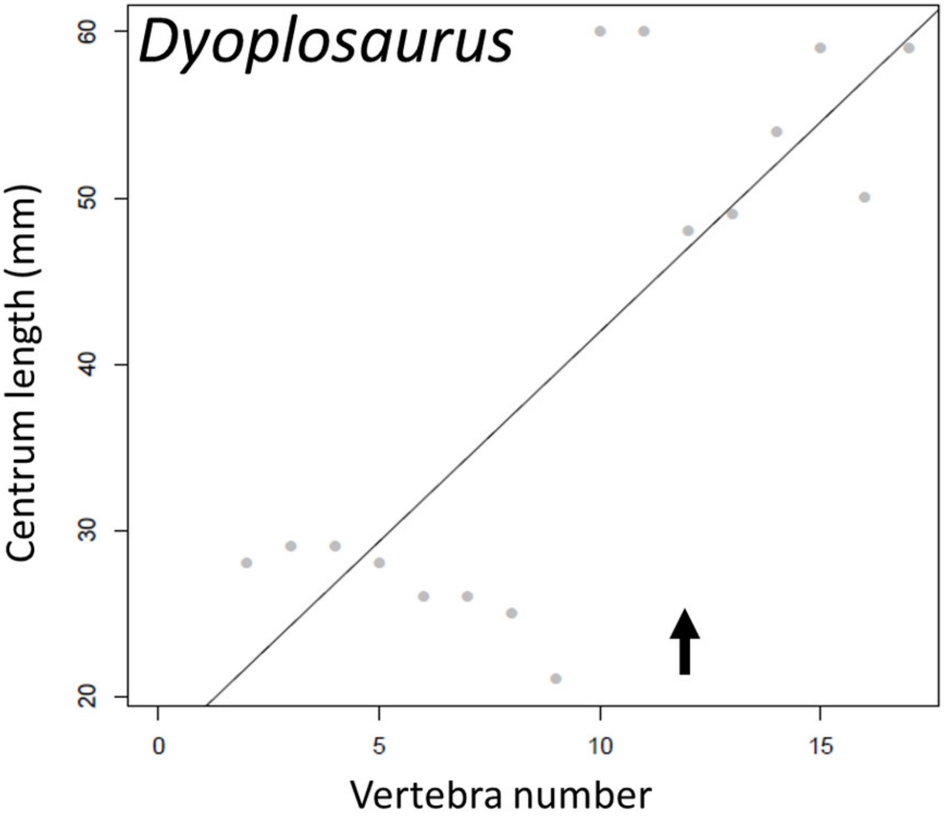

Dyoplosaurus
Centrum length (mm)
20
30
40
50
60
0
5
10
15
Vertebra number

Figure 9

Regressions for centrum lengths within the tails for members of the Ceratopsidae.

The first two specimens of *Psittacosaurus* are from the AMNH and the two specimens of *Leptoceratops* are from the CMN.

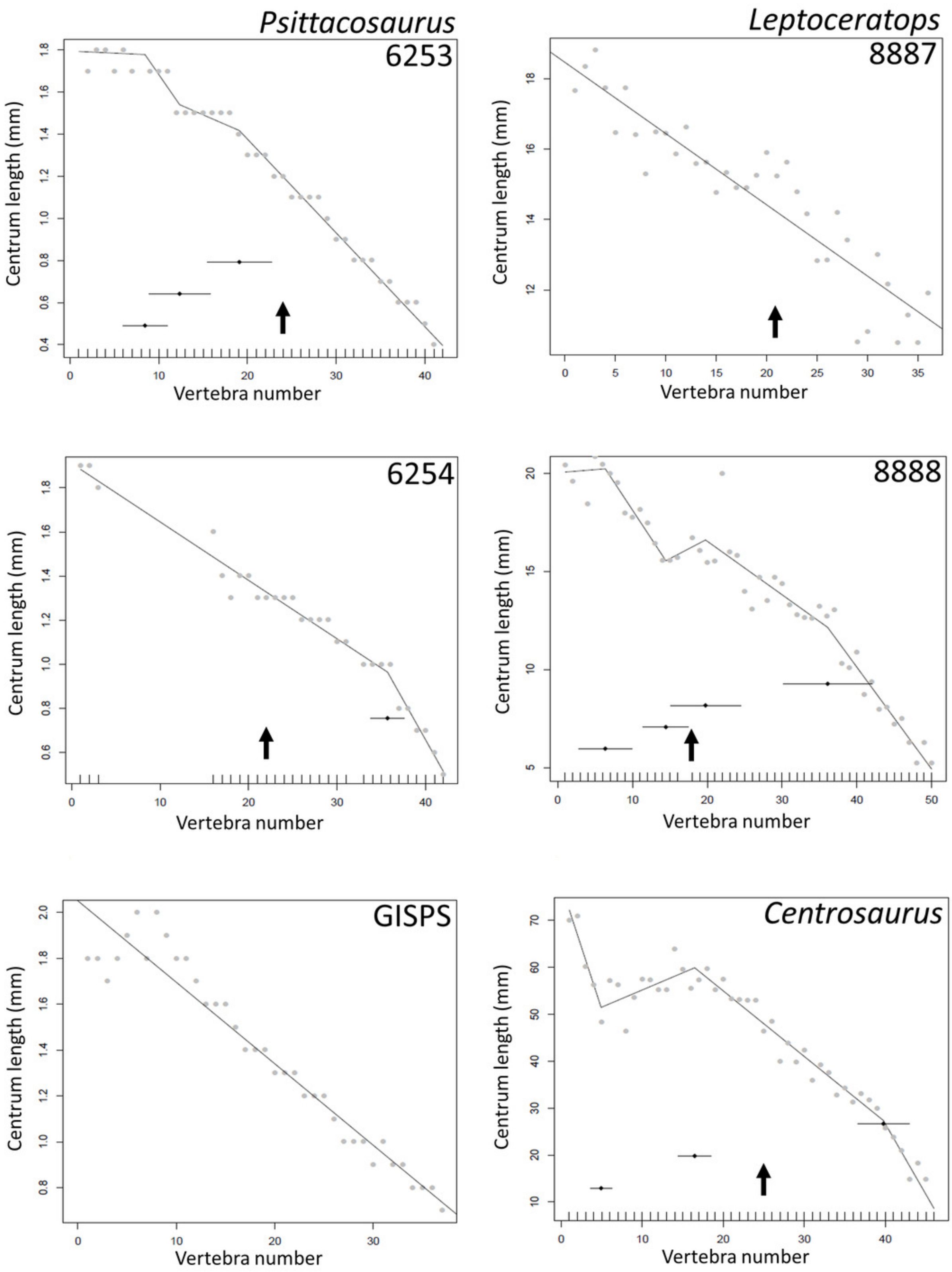
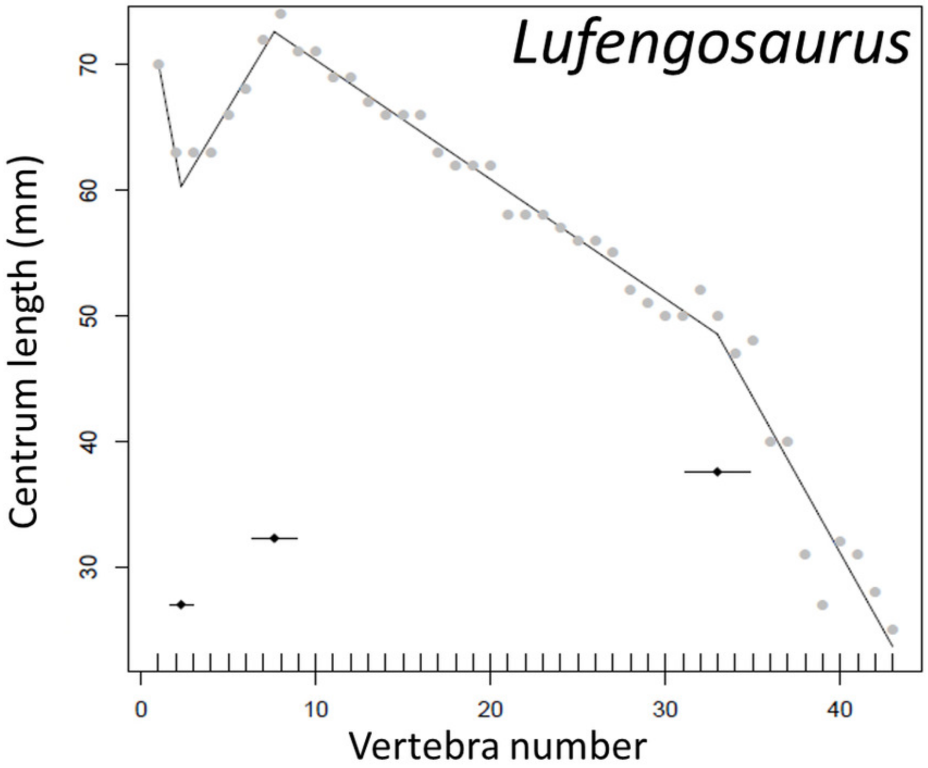

Psittacosaurus
6253
Centrum length (mm)
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
0
10
20
30
40
Vertebra number
Leptoceratops
8887
Centrum length (mm)
12
14
16
18
0
5
10
15
20
25
30
35
Vertebra number
6254
Centrum length (mm)
0.6
0.8
1.0
1.2
1.4
1.6
1.8
0
10
20
30
40
Vertebra number
8888
Centrum length (mm)
5
10
15
20
0
10
20
30
40
50
Vertebra number
GISPS
Centrum length (mm)
0.8
1.0
1.2
1.4
1.6
1.8
2.0
0
10
20
30
Vertebra number
Centrosaurus
Centrum length (mm)
10
20
30
40
50
60
70
0
10
20
30
40
Vertebra number

Figure 10

Regressions for centrum lengths within the tails for non-sauropodan members of the Sauropodomorpha.

Patterns of centrum lengths for a Jurassic and Triassic saruopodomorph.


Lufengosaurus
Centrum length (mm)
30
40
50
60
70
Vertebra number
0
10
20
30
40

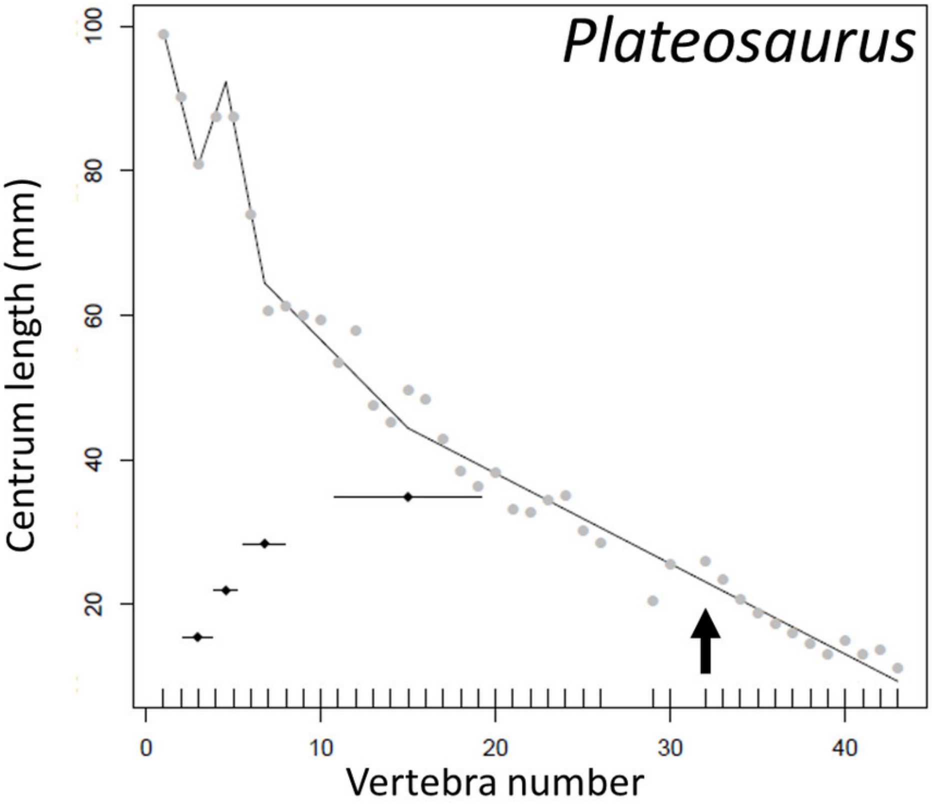

Plateosaurus
Centrum length (mm)
20
40
60
80
100
Vertebra number
0
10
20
30
40

Figure 11

Regressions for centrum lengths within the tails for members of the Theropoda.

Centrum length patterns for non-maniraptoran theropods.

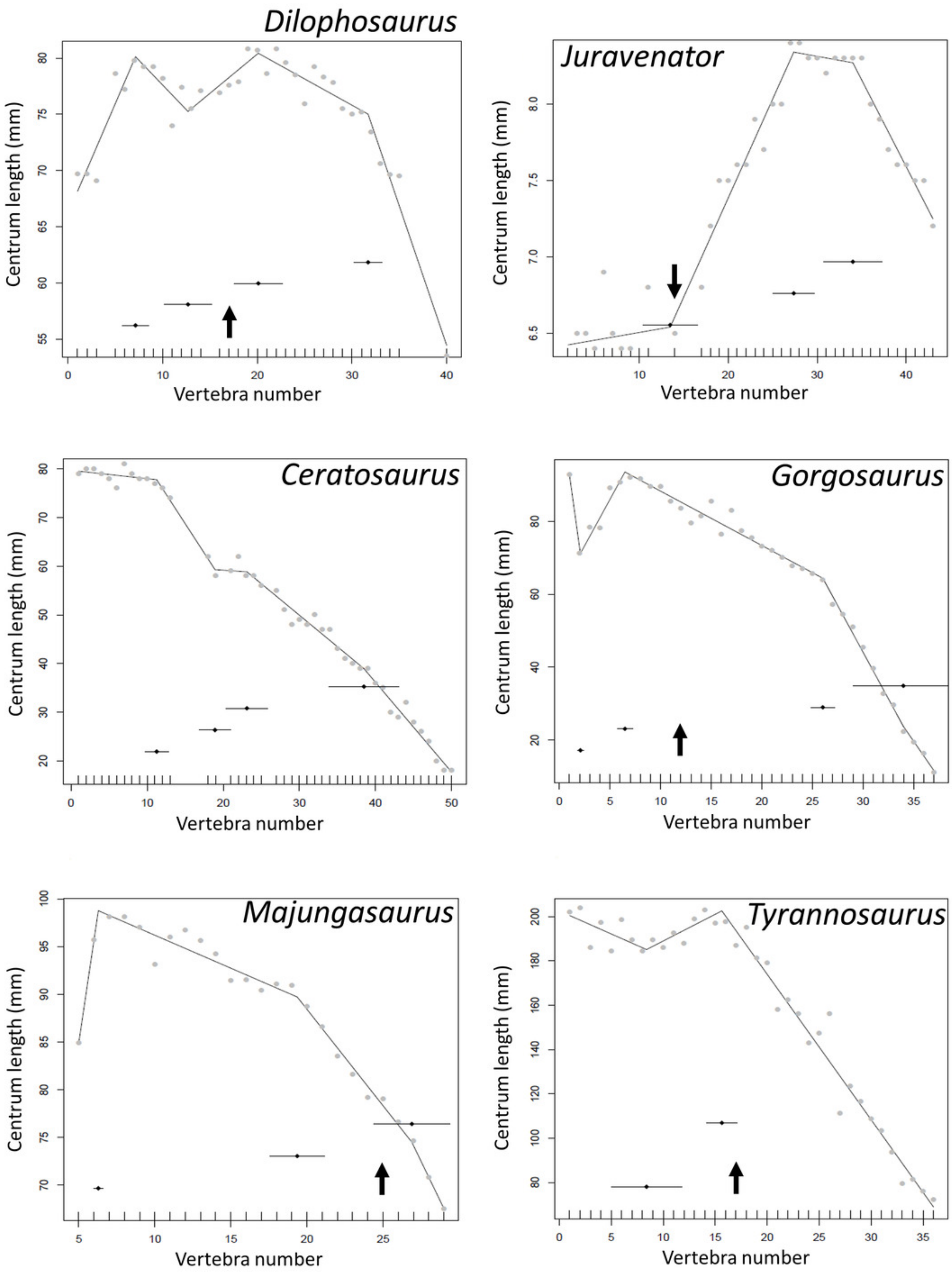
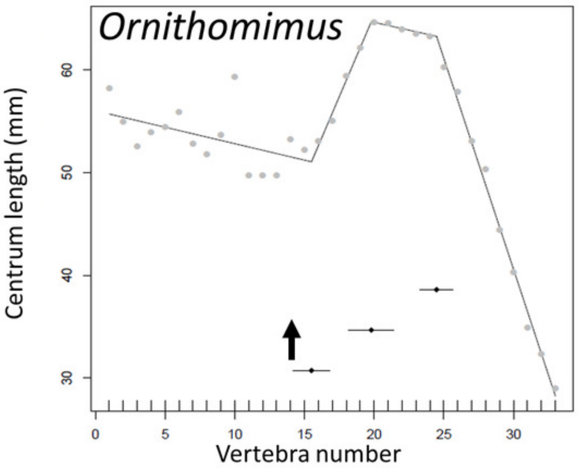
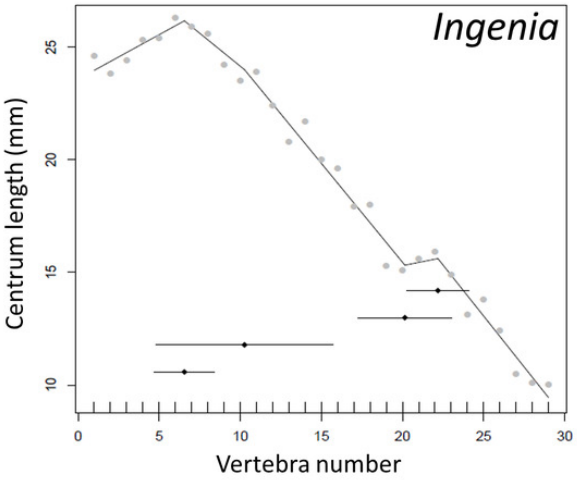

Dilophosaurus
Centrum length (mm)
55
60
65
70
75
80
0
10
20
30
40
Vertebra number
Juravenator
Centrum length (mm)
6.5
7.0
7.5
8.0
10
20
30
40
Vertebra number
Ceratosaurus
Centrum length (mm)
20
30
40
50
60
70
80
0
10
20
30
40
50
Vertebra number
Gorgosaurus
Centrum length (mm)
20
40
60
80
0
5
10
15
20
25
30
35
Vertebra number
Majungasaurus
Centrum length (mm)
70
75
80
85
90
95
100
5
10
15
20
25
Vertebra number
Tyrannosaurus
Centrum length (mm)
80
100
120
140
160
180
200
0
5
10
15
20
25
30
35
Vertebra number

Figure 12

Regressions for centrum lengths within the tails for members selected non-paravain Maniraptora.

Regressions for centrum lengths for an ornithomimid and two oviraptorosaurs


Ornithomimus
Centrum length (mm)
30
40
50
60
Vertebra number
0
5
10
15
20
25
30


Ingenia
Centrum length (mm)
10
15
20
25
Vertebra number
0
5
10
15
20
25
30

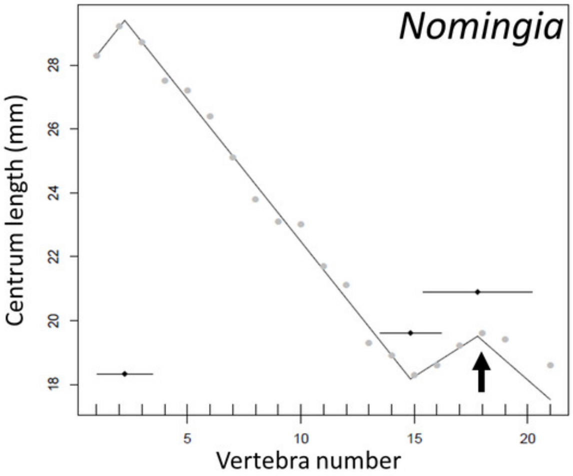

Nomingia
Centrum length (mm)
18
20
22
24
26
28
Vertebra number
5
10
15
20

Figure 13

Regressions for centrum lengths within the tails for members of the Dromaeosauridae.

The different specimens of *Velociraptor* can be identified by their museum prefixes.

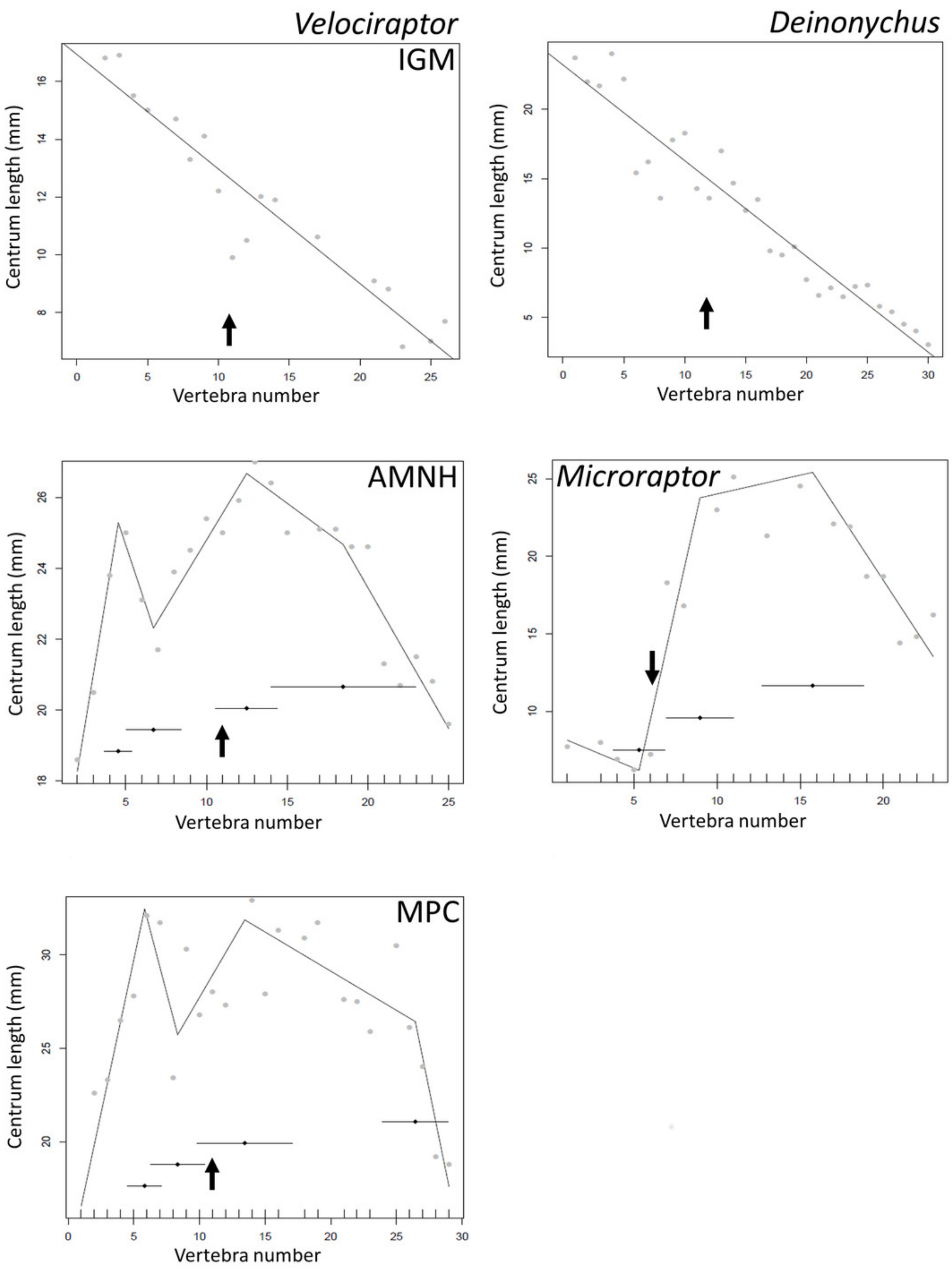
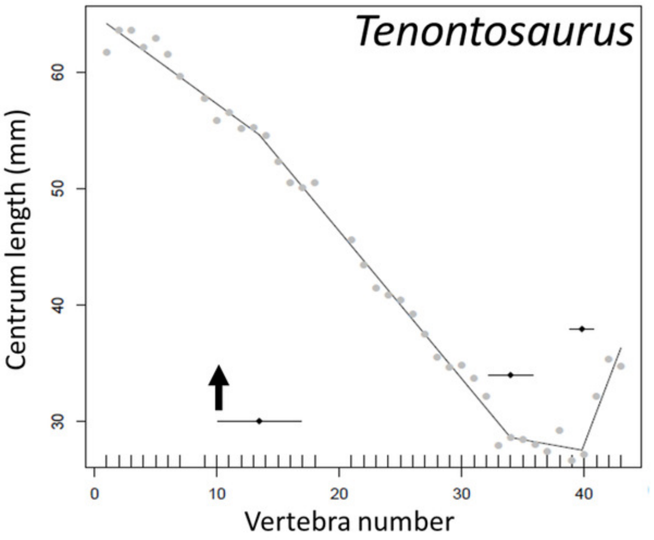
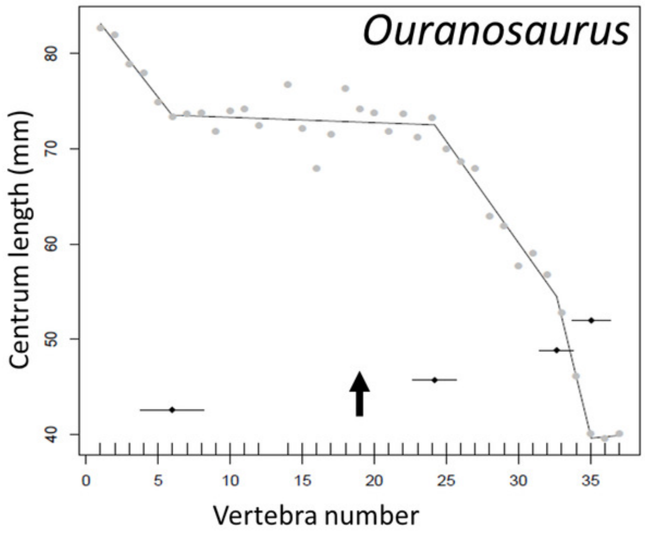

Velociraptor
IGM
Centrum length (mm)
8
10
12
14
16
0
5
10
15
20
25
Vertebra number
Deinonychus
Centrum length (mm)
5
10
15
20
0
5
10
15
20
25
30
Vertebra number
AMNH
Centrum length (mm)
18
20
22
24
26
5
10
15
20
25
Vertebra number
Microraptor
Centrum length (mm)
10
15
20
25
5
10
15
20
Vertebra number
MPC
Centrum length (mm)
20
25
30
0
5
10
15
20
25
30
Vertebra number

Figure 14

Regressions for centrum lengths within the tails for members selected non-hadrosauroid iguanodontians.

Centrum length patterns for three iguanodonts.


Tenontosaurus
Centrum length (mm)
30
40
50
60
0
10
20
30
40
Vertebra number


Ouranosaurus
Centrum length (mm)
40
50
60
70
80
0
5
10
15
20
25
30
35
Vertebra number

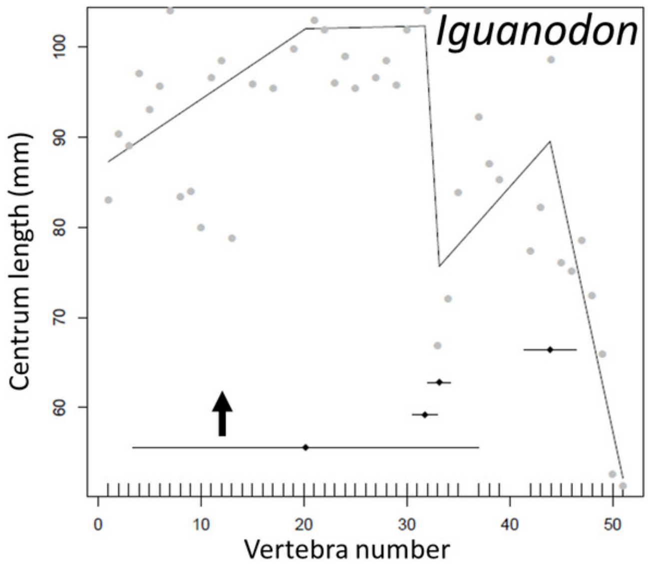
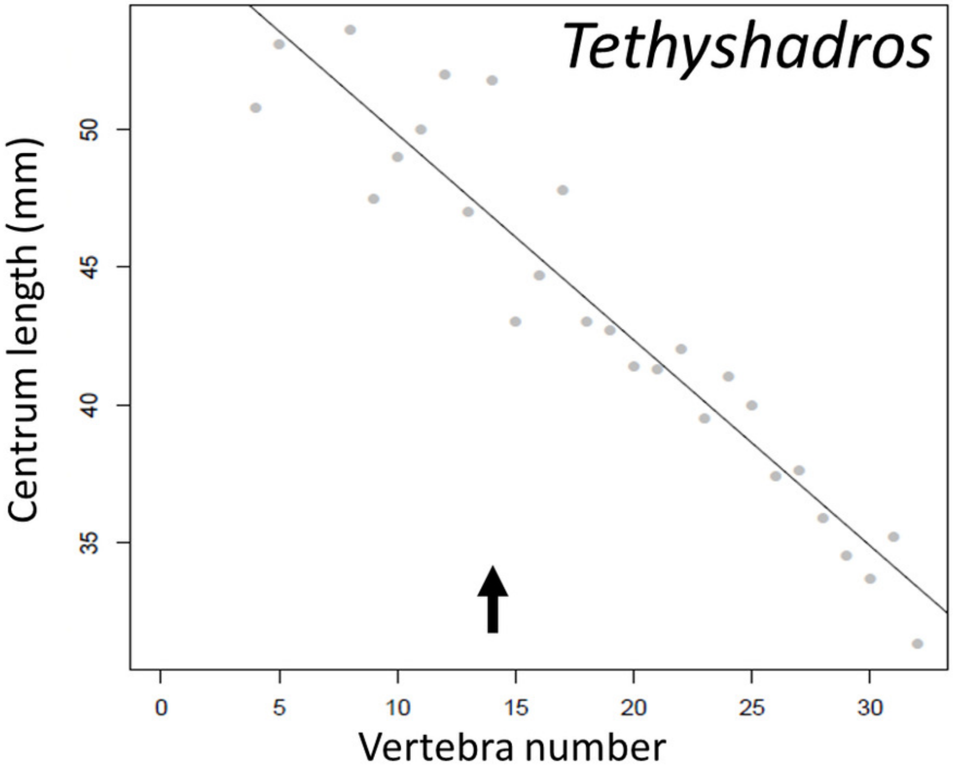

Iguanodon
Centrum length (mm)
60
70
80
90
100
0
10
20
30
40
50
Vertebra number

Figure 15

Regressions for centrum lengths within the tails for members selected Hadrosauridae.

Centrum length patterns for two hadrosaurs.


Tethyshadros
Centrum length (mm)
35
40
45
50
0
5
10
15
20
25
30
Vertebra number

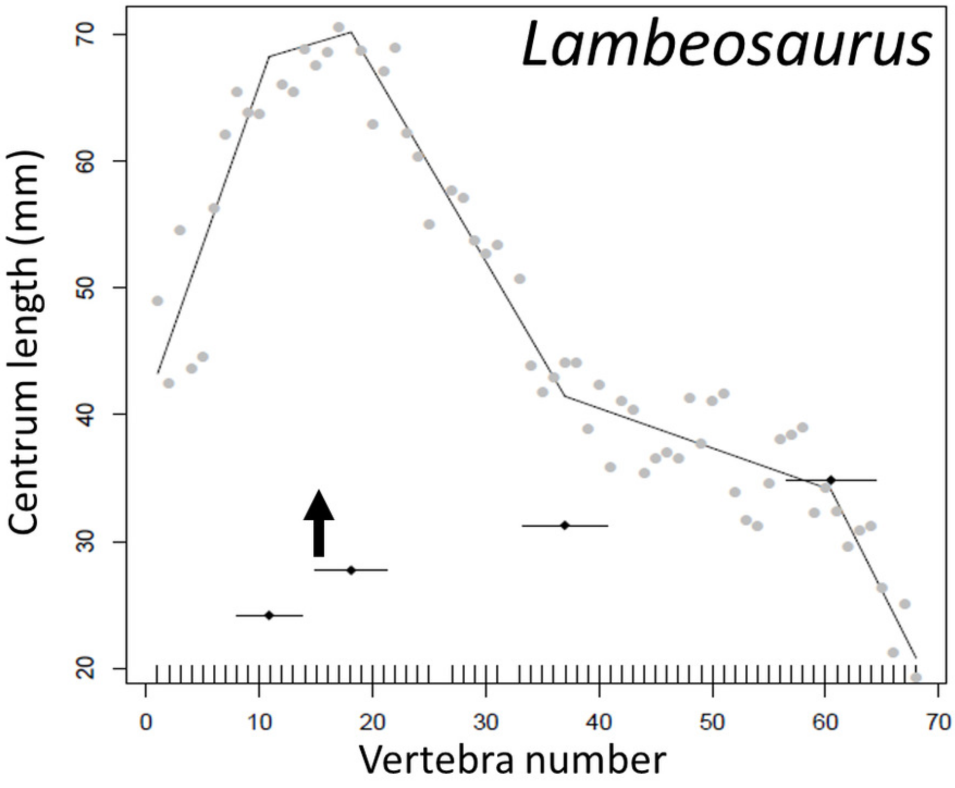
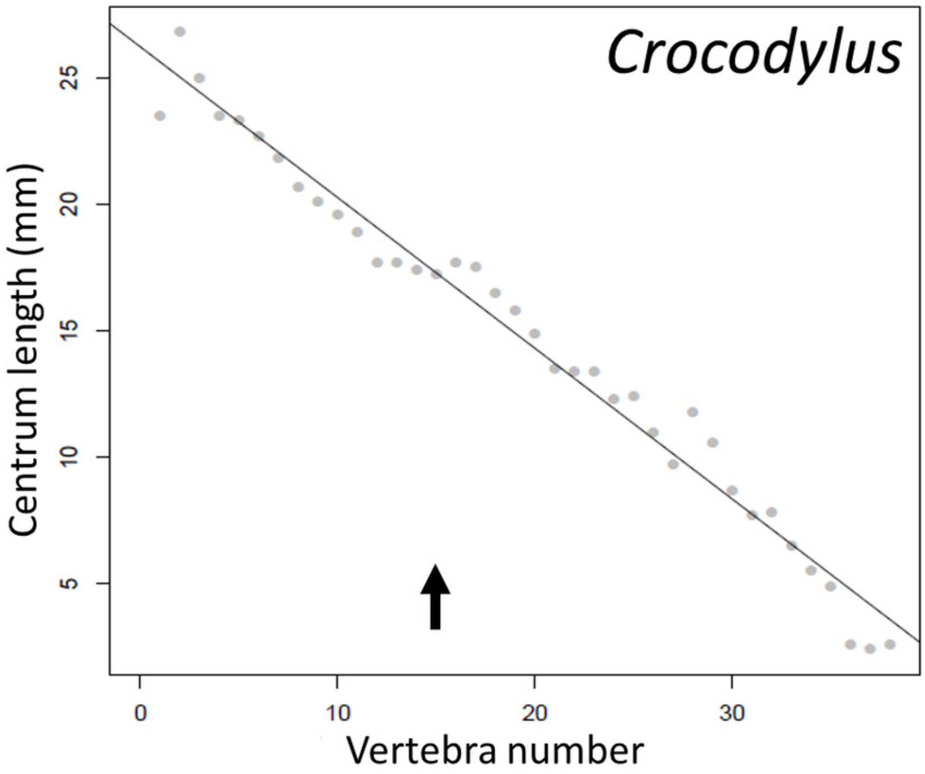
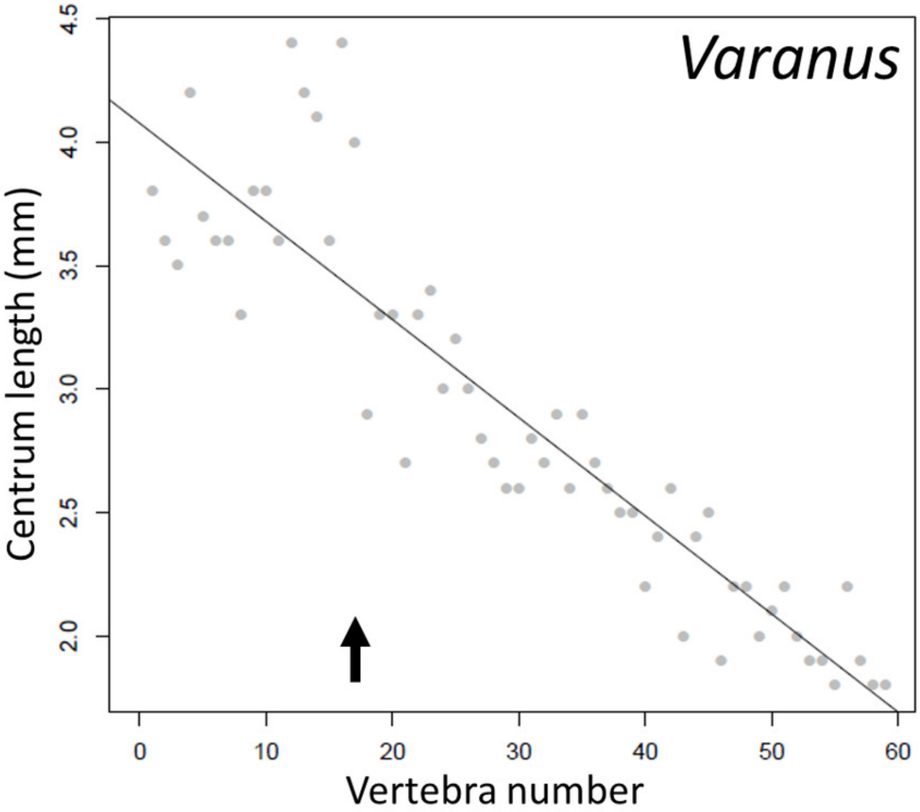

Lambeosaurus
Centrum length (mm)
20
30
40
50
60
70
0
10
20
30
40
50
60
70
Vertebra number

Figure 16

Regressions for centrum lengths within the tails for two non-dinosaurian reptiles

Centrum length patterns for *Crocodylus niloticus* and *Varanus nilitocus*.


Crocodylus
Centrum length (mm)
5
10
15
20
25
0
10
20
30
Vertebra number


Varanus
Centrum length (mm)
2.0
2.5
3.0
3.5
4.0
4.5
0
10
20
30
40
50
60
Vertebra number