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

First revision

Guidance from your Editor

Please submit by **25 Aug 2020** for the benefit of the authors .

Structure and Criteria
Please read the 'Structure and Criteria' page for general guidance.

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files
Download and review all files from the materials page.

1 Tracked changes manuscript(s)
1 Rebuttal letter(s)
17 Figure file(s)
1 Raw data file(s)

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- ✓ Original primary research within Scope of the journal.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ All underlying data have been provided; they are robust, statistically sound, & controlled.
- ✓ Speculation is welcome, but should be identified as such.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	***Example***
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

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

David W E Hone Corresp., 1 , **W. Scott Persons** 2 , **Steven C Le Comber** 1

1 School of Biological and Chemical Sciences, Queen Mary University of London, London, United Kingdom

2 Mace Brown Museum of Natural History, College of Charleston, Charleston, South Carolina, United States

Corresponding Author: David W E Hone
Email address: dwe_hone@yahoo.com

The tails of non-avian dinosaurs varied considerably in terms of overall length, total number of vertebrae, and 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.

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

David W. E. Hone[1], W. Scott Persons IV[2], Steven Le Comber[1]

1. School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London, E1 4NS, UK.
2. Mace Brown Museum of Natural History, College of Charleston, Charleston, South Carolina 29424, USA

Corresponding Author:
David W. E Hone
School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London, E1 4NS, UK Email address: d.hone@qmul.ac.uk

Abstract

The tails of non-avian dinosaurs varied considerably in terms of overall length, total number of vertebrae, and 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.

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, the osteological caudal anatomy of dinosaurs has had far less attention than most other major anatomical regions.

A key issue for their study, 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, such as estimates of the total length of specimens.

Studies on dinosaur tails have often focused on tails as flexible structures (Pittman et al., 2013) to support large 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 (e.g., Persons and Currie 2011a, b; Cau and Serventi 2017), and, most frequently, the 'transition point' of the lateral processes (Russell, 1972; Gauthier, 1986; 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. Nevertheless, when compared to vertebrae from elsewhere in the axial column, caudal vertebrates are generally simplified in overall form.

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. Recently, Nuñez Demarco et al. (2018) demonstrated a general pattern of either decreasing lengths of vertebrae along the tail, or an increase in length to the midpoint, followed by a decrease for a number of extant reptiles. They similarly demonstrated a reduced in the length of caudal vertebrae along the distal tail of the extinct *Mesosaurus*, though some individuals showed stability in the lengths distally (Nuñez Demarco et al., 2018).

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). Having short vertebrae means you have more flexing points per unit of length. ~~So, a~~ three meter long tail with thirty vertebrae is more flexible than a three meter ~~stretch of~~ tail with only twenty vertebrae (everything else being equal). But a tail with a total number of thirty vertebrae will be able to achieve a greater coil if it is longer (i.e. has longer individual vertebrae).

It has been argued that dorsal vertebra proportions are good correlates of absolute body size in tetrapod (see Currie 1978 for a review), but no similar argument has been made for caudal vertebrae. 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 vary considerably, even in mammals – both in terms of caudal count and total length (e.g. Garland, 1985; Cavallini, 1995; Alroy, 2019) – suggesting it is relatively free of such constraints.

Such possible variation in function and morphology has yet to be explored. Indeed, changes in caudal centra length for dinosaurs 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 pattern of decrease in length in successive vertebrae. Specifically, the presence of the lateral processes are known to be associated with a major change in tail function (the presence of the caudofemoralis musculature) and we, therefore, predict that the posterior loss of the lateral processes correlates with a change in centrum lengths. It is expected that testing these hypotheses will reveal variation important to the function and evolution of tails in subclades and locomotor regimes within Dinosauria.

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; MB.R. fossil reptiles collection of MfN (Museum für Naturkunde) Berlin; MNA Museum of Northern Arizona, Flagstaff; MPC Mongolian Paleontological Centre, Mongolian Academy of Sciences, Ulan Baator; NHMUK 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 ~~marginal~~ 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 (this trait remain useful even in procoelous vertebrae, because the extent of the rounding exceeds that observed elsewhere in the series) 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. Nearly complete 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 many cases the live animals may have possessed intervertebral discs that would have increased tail length, but these cannot be easily estimated and so were simply excluded (though see also Rothschild et al., 2020 who argue for their absence).

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 – Campione & Evans, 2012) are stronger correlates of mass, femur length is appropriate for such datasets, and length was the only reliable measurement for samples from the literature or from specimens that are taphonomically distorted. To examine the relationship between tail length and body size, we compared snout to sacrum length and tail length using a simple linear least-squares regression. Snout-sacrum length was taken as the combined length of the skull and every cervical, dorsal and sacral centrum (see Hone, 2012 for further details). 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, thyreophorans), 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 seen with *Diplodocus*, for example. 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 the diplodocid sauropod *Barosaurus* AMNH 6341 (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 these datasets (though it is included for the section on individual centra lengths).

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).

The data is unevenly distributed with a bias towards small theropods (a taphonomic bias from Lagerstaetten deposits) and likely further biases from interest in the maniraptoran-avian transition, with a bias against sauropodomorphs (large animals with numerous tail vertebrae that would be difficult to be buried as a complete specimen). Thus, for the data on snout-sacrum vs complete tail length, there were 16 ornithischians (of which seven were ceratopsians), 12 theropods (of which seven were deinonychosaurs), but only three sauropodomorphs.

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 if there were transitions in centrum length (break points), and if so, how many. These length transitions were then compared with the boundary between the muscular and less-muscular parts of the tail (the 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 section covers vertebrae 21-35, the third section covers vertebrae 35-67 and the final section covers vertebra 67-84 (Fig. 2). Clearly, however, in some cases a simple linear regression will provide a better fit to the data. Because of some debate over the best way to assess goodness of fit for segmented regressions (e.g., Hall et al., 2013*)* the analysis was started with a Davies test (Davies, 2002) 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). This allows us an independent test of whether a segmented regression is justified, meaning that we were able to use one where the data support it (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.

In one case (*Dyoplosaurus*) the Davies test indicated that a simple linear model was appropriate but visual inspection of the fit indicated that there are in fact two separate groups of vertebrae. The breakpoint models fitted by *segmented* assume a continuous relationship but in this case it was clear that a discontinuous model ~~would be best~~. Therefore, one was fitted by classifying the vertebrae into two groups and then including this as a factor in a linear model plus the interaction term with vertebra number.

Results

Tail length vs snout-sacrum length

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 model suggests that tail length is an extremely poor predictor of snout to sacrum length across dinosaurs (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.

The same poor prediction of snout-sacrum length by tail length is retained (linear regression: F1,16 = 0.01, p = 0.91) if we attempt to minimise problems due to ~~intraspecific~~ (ontogenetic) scaling or phylogenetic bias (where there are multiple specimens from some species that are therefore over-represented) 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~~. This pattern 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.

~~Fundamental~~ 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. ~~In other words~~, dinosaur tails do not show simple patterns of change in centrum lengths but typically exhibit multiple distinct regions. 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 with~~ high variation between multiple specimens of a single population of one species (e.g. *Coelophysis* – Fig. 4). The details of ~~these~~ for various species and clades are considered in more detail below.

Break points ~~and musculature~~

Where multiple measurements were taken from one hadrosaur tail as a test of consistency of measurements, the congruence was good between break points produced from direct measurements of the specimen and a photograph. 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. 5). This suggests that the measurements taken from photographs for various specimens will yield accurate data.

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). This suggests that there is a ~~genuine connection~~ between the end of the lateral processes (and by extension the termination of the *caudofemoralis* muscles) and a change in length of the centra in the tail.

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. 7), *Leptoceratops, Centrosaurus* (both Fig. 8)*, Lufengosaurus* (Fig. 9)*, Apatosaurus*, *Camarasaurus* (both Fig. 2), *Gorgosaurus, Tyrannosaurus* (both Fig. 10), *Ornithomimus, Nomingia* (both Fig. 11), *Microraptor,* and *Velociraptor* (both Fig. 12). ~~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 far from this pattern (e.g., *Dilophosaurus* (Fig. 10), *Ingenia* (Fig. 11)*, Ouranosaurus* and *Lambeosaurus* (both Fig. 13)). It is possible 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 seem to conform to the pattern, it cannot be confirmed. In the case of *Dyoplosaurus* the discontinuous model was the best supported (AIC simple linear regression. = 121.7, AIC discontinuous model = 96.0) and so this was retained (Fig. 7).

Discussion

Overall lengths of dinosaurian tails

Dinosaur tail lengths vary widely overall and the correlations between tail length and snout-sacrum lengths for complete tails is poor. 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 clades represented by few specimens (e.g., Scansoriopterygidae). Dinosaur tails were also likely evolutionally plastic given the highly derived forms seen in clades such as ankylosaurus and diplodocids. ~~Similarly, multiple lineages show adaption of the tail to specific functions (or specific combinations of functions) such as defence and socio-sexual signaling 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 multiple environments. 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.

~~However,~~ other taxa deviate considerably from the short-long-shortening pattern described above (e.g. *Plateosaurus* (Fig. 8)*,* *Juravenator* (Fig. 10))~~;~~ ~~indeed~~ the caudals of *Coelophysis* tend to increase in length for much of the series (Fig. 4). 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 of a species and between genera (Fig. 12). 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~~, show a level of consistency not seen in other groups (Figs. 4, 12). 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. 11), though the specimen here is a young juvenile and it is possible that the tail changes during ontogeny. ~~That said,~~ Chiappe and Göhlich (2010) noted that the caudal length pattern of *Juravenator* (a stable series, then a series of short centra, then a series of long centra, and then a series of shorter centra 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. 5).

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. 8), three specimens of *Archaeopteryx* (Fig. 4), and two tyrannosaurids (Fig. 10) 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. 12).

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 of 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) of dinosaurs 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. 5) as determined by the changes in regression lines (e.g. *Lambeosaurus* (Fig. 13)*, Juravenator, Gorgosaurus, Tyrannosaurus* (all Fig. 10)*, Ornithomimus* (Fig. 11)).

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. 9) and *Nomingia* (Fig. 11). 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. Posterior to the short centra at the very base of the tail, 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, sense, in the absence of other anatomical changes, longer vertebra lead to a reduction in intervertebral flexure points per unit of length. This would improve the efficiency of the caudofemoralis muscles as this stiffness would reduce energy loss though lateral movements between vertebrae and ensure that most of the effort of contracting the muscles led to anterior pull on the femur and not flexing the tail laterally.

Posterior to the transition point, the requirement for ~~great~~ lateral stiffness is presumably relaxed and thus lead to the simple pattern of general reduction in size of successive centra moving posteriorly. ~~Of course~~, many taxa independently evolved post-transition-point adaptations for increasing caudal stiffens, such as the relatively elongated centra and extensive zygopotheses of tetanurans, the caudal rods of dromaeosaurs, or the pygostyles of various maniraptorans. Simple selection for reduction in mass posteriorly (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. That is seen here in the data for *Varanus* and *Crocodylus* (SI Fig. 4) and this pattern was also recorded from some other extant and extinct reptiles, and even synapsids by Nuñez Demarco et al. (2018) suggesting this may be a common feature of early amniotes ~~(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 anterior motion of the tail would also affect any more posterior 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~~. 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, which contribute to the origin of the caudofemoralis. This would afford far less muscle attachment than in the ~~immediately posterior~~ section of the tail. Additionally, the bending moment of the caudofemoralis would be proportional to the small sine of the angle between the origins of the caudofemoralis and its lines of action, making the most anterior vertebrae less strongly influenced.

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. 4; *Plateosaurus*, Fig. 9), 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 and anklosaurs, hyposphene-hypantra articulations in some sauropods and alvarezsaurs, 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 locomotor 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, guessing at what number of vertebrae a tail will end is difficult. 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”. Similarly, pygostyles of some theropods (which can reduce very rapidly in size along their length) could also be misleading, as, if only the proximal part were preserved, it would erroneously suggest a much longer.

~~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) for *Amurosaurus*, 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. This pattern ~~in form~~ suggests a ~~standard dinosaurian pattern in tail function~~, where (1) the very base of the tail was flexible and allowed the large remaining posterior portion of the tail to be swung as a collective whole, (2) shortly past the tail base there was a zone of relative stiffness that supported the caudofemoralis musculature, and (3) after the termination of the caudofemoralis and for a highly variable distance, the remaining vertebrae tapered to a reduced size.

While length of centrum is the most relevant measure of an individual vertebrae's contribution to total tail length, numerous other traits have the potential to ~~substantially~~ influence basic aspects of caudal function, including lateral flexibility and the workings of the caudofemoralis. Future studies of variation patterns in other traits (such as centrum width and zygapophyseal articulation) ~~have the potential to support or dispute the functional interpretations offered here and~~ will ~~likely~~ refine these general observations. Although developed in order to investigate dinosaur tails, the methods used here to separate out groups of similar units as part of a series may be widely applicable to assessments of any extinct and extant taxa exhibiting repeating anatomical units (e.g. the dimensions of any vertebral series, scalation, or body segments in anilid or arthropod invertebrates).

Acknowledgements

We wish to thank the numerous colleagues who provided papers, discussions, and details of specimens with complete tails that are buried in the literature and research collections: Jordan Mallon, Matthew Herne, Susie Maidment, Corwin Sullivan, Fabio Dalla Vecchia, Andrea Cau, Victoria Arbour, Mickey Mortimer, Phil Currie, Matt Wedel, Pascal Godefroit and Chris Rogers. For access to specimens we thank Sandra Chapman and Fang Zheng. We thank Mike Habib for discussion of tail evolution and stiffening and Rob Knell for assistance with the statistics. We also thank Victoria Arbour, Heinrich Mallison, Eric Snively, Susie Maidment and David Polly for comments on an earlier version of this manuscript and Mark Young for handling it as editor.

References

Akaike H. 1974. A new look at the statistical model identification. *IEEE Transaction of Automatatic Control* 19:716–23.

Allen V, Paxton H, Hutchinson JR. 2009. Variation in center of mass estimates for extant sauropsids and its importance for reconstructing inertial properties of extinct archosaurs. *Anatomical Record* 292:1442–1461.

Alroy J. 2019. Small mammals have big tails in the tropics. *Global Ecology and Biogeography*, 28:1042-1050.

Arbour VM. 2009. Estimating impact forces of tail club strikes by ankylosaurid dinosaurs. *PLoS ONE* 4:e6738.

Borsuk-Bianka M. 1977. A new camarasaurid sauropd *Opisthocoelicaudia skarzynskii*, gen. n. sp. n. from the Upper Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 37:5–64.

Campione NE, Evans DC. 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC biology* 10:60.

Cau A, Serventi P. 2017. Origin attachments of the caudofemoralis longus muscle in the Jurassic dinosaur Allosaurus. *Acta Palaeontologica Polonica* 62:273–277.

Cavallini, P. 1995. Variation in the body size of the red fox. *Annales Zoologici Fennici* 32:421–427.

Chiappe LM, Göhlich UB. 2010. Anatomy of *Juravenator starki* (Theropoda: Coelurosauria) from the Late Jurassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen* 258:257–296.

Currie PJ. 1978. The orthometric linear unit. *Journal of Paleontology* 52: 964-971.

Dalla Vecchia F. 2009. *Tethyshadros insularis*, a new hadrosauroid dinosaur (Ornithischia) from the Upper Cretaceous of Italy. *Journal of Vertebrate Paleontology* 29:1100–1116.

Davies RB. 2002. Hypothesis testing when a nuisance parameter is present only under the alternative: linear model case. *Biometrika* 89:484–489.

Garland T Jr. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *Journal of Zoology* 207:425–439.

Gauthier JA. 1986. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* 8:1-55.

Gatesy SM. 1990. Caudefemoral musculature and the evolution of theropod locomotion. *Paleobiology* 16:170–186.

Gatesy SM, Dial KP. 1996. From frond to fan: *Archaeopteryx* and the evolution of short-tailed birds. *Evolution* 50:2037–2048.

Gatesy SM, Thomason JJ. Functional morphology in vertebrate paleontology. *Functional evolution of the hindlimb and tail from basal theropods to birds*. 1995:219–34.

Gilmore CW. 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum* 11:175–271.

Hall AR, Osborn DR, Sakkas N. 2013. Inference on Structural Breaks using Information Criteria. *The Manchester school of economic and social studies* 81*:*54–81.

Head JJ, David Polly P. Dissociation of somatic growth from segmentation drives gigantism in snakes. *Biology Letters* 22:296–8.

Hone DWE. 2012. Variation in the tail length of non-avian dinosaurs. *Journal of Vertebrate Paleontology* 32:1082–1089.

Horner JR, Weishampel DB, Forster CA. 2004. Hadrosauridae. In: Weishampel DB, Dodson P, Osmólska H, eds. The Dinosauria. Berkeley: University of California Press, 438–465.

Hutchinson JR, Gatesy SM. 2001. Bipedalism. *Encyclopedia of Life Sciences* 1-6.

Hutchinson JR, Ng-Thow-Hing V, Anderson FC. 2007. A 3D interactive method for estimating body segmental parameters in animals: application to the turning and running performance of *Tyrannosaurus rex*. *Journal of Theoretical Biology* 246:660–680.

Lauters P, Bolotsky YL, Van Itterbeeck J, Godefroit P. 2008. Taphonomy and age profile of a Latest Cretaceous dinosaur bone bed in Far Eastern Russia. *Palaios* 23:153–162.

Libby T, Moore TY, Chang-Siu E, Li D, Cohen DJ, Jusufi A, Full RJ. 2012. Tail-assisted pitch control in lizards, robots and dinosaurs. *Nature* 481:181–184.

Lull RS, Wright NE. 1942. Hadrosaurian dinosaurs of North America. *Geological Society of America Special Papers* 40.

Mallison H. 2011. Defense capabilities of *Kentrosaurus aethiopicus* Hennig, 1915. *Palaeontologia Electronica* 14:1–25.

McIntosh JS. 2005. The genus *Barosaurus* Marsh (Sauropoda, Diplodocidae). In Tidwell V, Carpenter K, eds. Thunder-lizards: the sauropodomorph dinosaurs Bloomington: Indiana University Press, 8-77.

Muggego VMR. 2003. Estimating regression models with unknown break-points. *Statistics in Medicine* 22:3055–3071.

Muggego VMR. 2008. segmented: an R Package to Fit Regression Models with Broken-Line Relationships. *R News* 8:20–25. URL http://cran.r-project.org/doc/Rnews/.

Nuñez Demarco P, Meneghel M, Laurin M, Piñeiro G. 2018. Was *Mesosaurus* a fully aquatic reptile?. *Frontiers in Ecology and Evolution* 6:p.109.

Persons WS, Currie PJ. 2011*a*. The tail of *Tyrannosaurus*: reassessing the size and locomotive importance of the M. caudofemoralis in non-avian theropods. *The Anatomical Record* 294:119–131.

Persons WS, Currie PJ. 2011*b*. Dinosaur speed demon: the caudal musculature of *Carnotaurus sastrei* and implications for the evolution of South American abelisaurids. *PLOS ONE* 6:e25763.

Persons WS, Currie PJ. 2012. Dragon tails: convergent caudal morphology in winged archosaurs. *Acta Geologica Sinica (English edition)* 86:1402–1412.

Persons WS, Currie PJ. 2014. Duckbills on the run, the cursorial abilities of hadrosaurs and implications for tyrannosaur avoidance strategies. In: Eberth DA, Evans DC eds. Hadrosaurs. Indiana University Press, Bloomington, Indiana. 449-458.

Persons WS, Currie PJ, Norrell MA. 2014. Oviraptorosaur tail forms and functions. *Acta Palaeontologica Polonica* 59:553–567.

Pittman M, Gatesy SM, Upchurch P, Goswami A, Hutchinson JR. 2013. Shake a tail feather: the evolution of the theropod tail into a stiff aerodynamic surface. *PLoS ONE* 8:e63115.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Rothschild BM, Depalma RA, Burnham DA, Martin L. 2020. Anatomy of a dinosaur—Clarification of vertebrae in vertebrate anatomy. *Anatomia, Histologia, Embryologia*.

Russell DA. Ostrich dinosaurs from the Late Cretaceous of western Canada. *Canadian Journal of Earth Sciences* 9:375–402.

Sereno PC. 1987. The ornithischian dinosaur *Psittacosaurus* from the Lower Cretaceous of Asia and the relationships of the Ceratopsia. *Ph.D. Dissertation, Columbia University*, New York, 554 pp.

Wake DB. 1979. The endoskeleton: the comparative anatomy of the vertebral column and ribs. *Hyman's comparative vertebrate anatomy*. 192:237.

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. The 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*). A) *Omeisaurus*, B) *Opsitocoelocaudia*, C) *Diplodocus*, D) *Apatosaurus* CM3018, E) *Apatosaurus* CM3378, F) *Camarasaurs*.

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 and demonstrate that while most cluster in the centre, there are extremes (from 1.3 to 12.4) and here the confidence intervals would be even wider. See also Table 1.

Figure 4. Regressions for centrum lengths within the tails for specimens of *Archaeopteryx* (A) BSPG1999I50, B) WDC CGS100 C) 11th Specimen) and *Coelophysis* (D) AMNH 7223, E) AMNH 7224, F) AMNH7229). *Archaeopteryx* is a rare genus for which numerous specimens with complete tails are known. Although the general pattern observed across the specimens is similar, the pattern of each specimen is distinct. Despite all three *Coleophysis* specimens coming from the same locality, their tails differ markedly from each other. The 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.

Figure 5. Segmented regressions for the indeterminate hadrosaur 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. The 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.

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). Abbreviations for listed specimens are as follows: Ap *Apatosaurus*, Cam *Camarasaurus*, Cen *Centrosaurus*, Coe *Coelophysis*, Dil *Dilophosaurus*, Dip *Diplodocus*, Gor *Gorgosaurus*, Ig *Iguanodon*, Jur *Juraventor*, Ken *Kentrosaurus*, Lam *Lambeosaurus*, Lep *Leptoceratops*, Maj *Majungasaurus*, Mic *Microraptor*, Nom *Nomingia*, Ome *Omeisaurus*, Opi *Opistocoelocaudia*, Orn *Ornithomimus*, Our *Ouranosaurus*, Pla *Plateosaurus*, Ps *Psittacosaurus* (1= AMNH 6253, 2 = AMNH 6254), Ten *Tenontosaurus*, Ty *Tyrannosaurus*, Vel *Velociraptor*

Figure 7. Regressions for centrum lengths within the tails for members of the Thyrophorea, A) *Kentrosaurus* , B) *Dyoplosaurus*. More than any other taxa in the study, the club bearing tail *Dyoplosaurus* would be expected to show a specialized pattern, and it does, although surprisingly the analysis did not recover break points in the series. The 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.

Figure 8. Regressions for centrum lengths within the tails for members of the Ceratopsidae. A) *Psittacosaurus* AMNH 6253, B) *Psittacosaurus* AMNH 6254, C) *Psittacosaurus* GiSPS 100/606, D) *Leptoceratops* CMN 8887, E) *Leptoceratops* CMN 8888), E) *Centrosaurus*. Relative to that of most other dinosaur groups considered, the ceratopsians pattern is closer to simple progressive tapering. The 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.

Figure 9. Regressions for centrum lengths within the tails for non-sauropodan members of the Sauropodomorpha, A) *Lufengosaurus,* B) *Plateosaurus*. While different patterns are recovered, both show long sections of the tail with a tapering pattern of centra lengths. The 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.

Figure 10. Regressions for centrum lengths within the tails for non-maniraptoran members of the Theropoda, A), *Dilophosaurus*, B) *Ceratosaurus*, C) *Majungasaurus*, D) *Juravenator*, E) *Gorgosaurus*, F) *Tyrannosaurus*. Note that patterns of the two tyrannosaurs, *Gorgosaurus* and *Tyrannosaurus*, are most similar to each other and that the pattern of *Juravenator* is the most dissimilar from all other theropods. The 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.

Figure 11. Regressions for centrum lengths within the tails for selected members of non-paravain Maniraptora A) *Ornithomimus* B) *Ingenia*, C) *Nomingia*. The two ovriaptorosaurs (B, C) show strongly tapering tails. The 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.

Figure 12. Regressions for centrum lengths within the tails for members of the Dromaeosaurida, A) *Velociraptor* IGM 100/25, B) *Velociraptor* AMNH 100-986, C) *Velociraptor* MPC 100/985), D) *Deinonychus*, E) *Microraptor*. The 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.

Figure 13. Regressions for centrum lengths within the tails for members selected non-hadrosauroid iguanodontians, A) *Tenontosaurus*, B) *Ouranosaurus*, C) *Iguanodon*) and hadrosaurs, D) *Tethyshadros*, E) *Lambeosaurus*). Despite their overall similarity in form and ecology there are considerable differences between the patterns seen between these taxa. The 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.

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.

SI Fig 4. Regressions for centrum lengths within the tails for two non-dinosaurian reptiles. Centrum length patterns for *Crocodylus niloticus* and *Varanus nilitocus*. Both display a simpler pattern than that typical of the considered dinosaurs with a relatively consistent decrease in centrum length along the caudal series. The transition point (where known) is indicated by an arrow.

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.

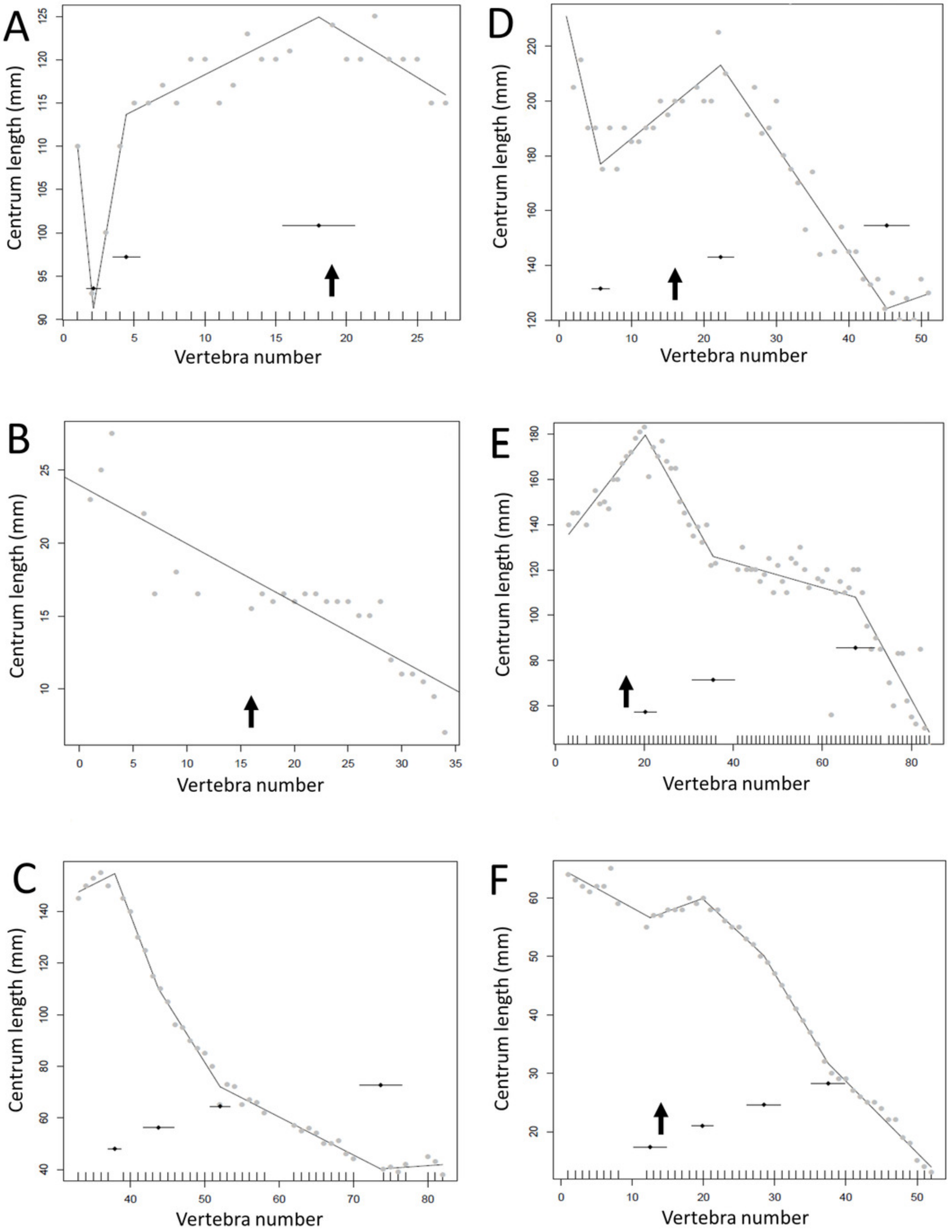

A
Centrum length (mm)
90
95
100
105
110
115
120
125
0
5
10
15
20
25
Vertebra number
D
Centrum length (mm)
120
140
160
180
200
220
0
10
20
30
40
50
Vertebra number
B
Centrum length (mm)
10
15
20
25
0
5
10
15
20
25
30
35
Vertebra number
E
Centrum length (mm)
60
80
100
120
140
160
180
0
20
40
60
80
Vertebra number
C
Centrum length (mm)
40
60
80
100
120
140
40
50
60
70
80
Vertebra number
F
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.

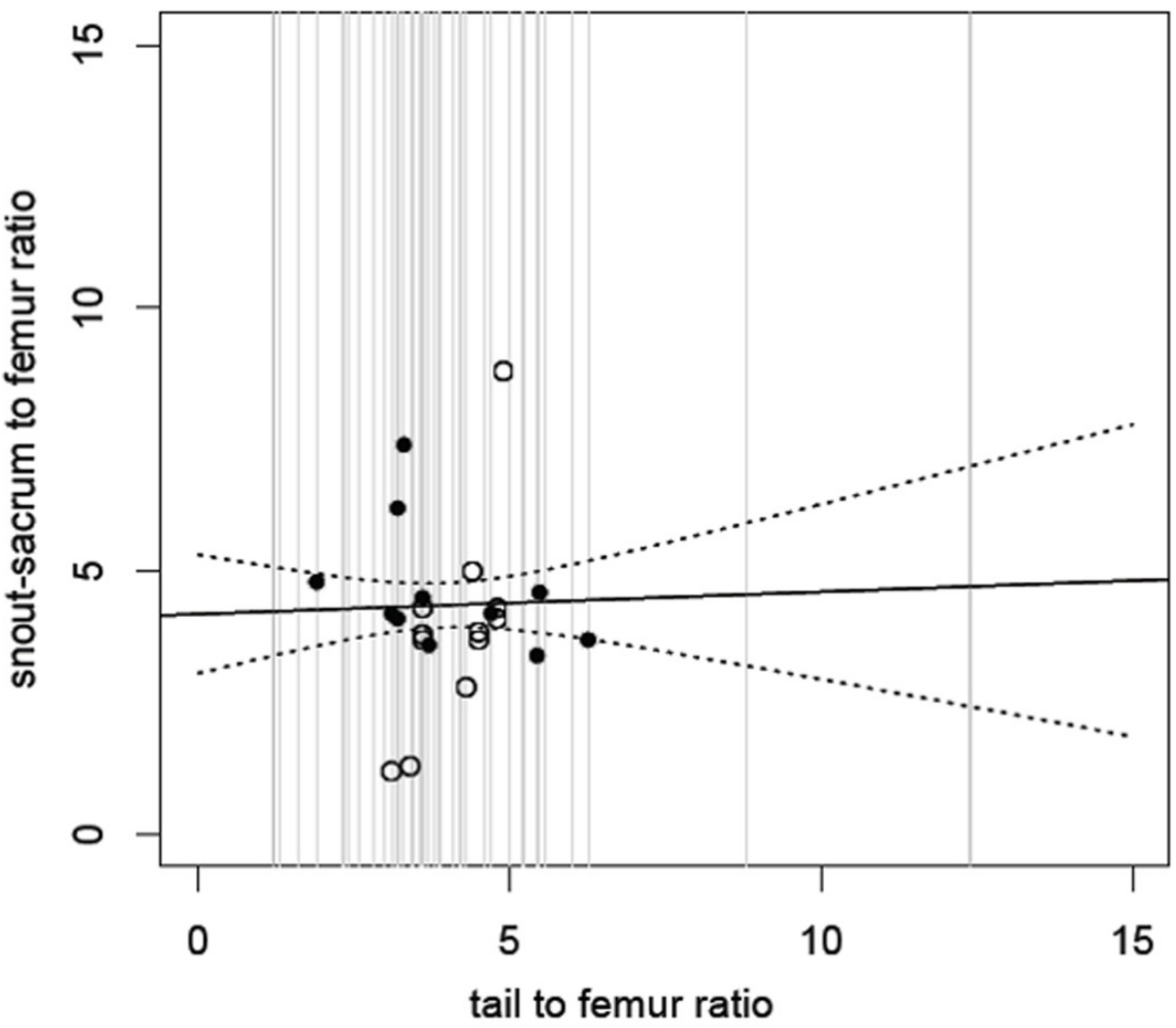

snout-sacrum to femur ratio
tail to femur ratio
0
5
10
15
0
5
10
15

Figure 4

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

The different specimens can be identified by their museum prefixes.

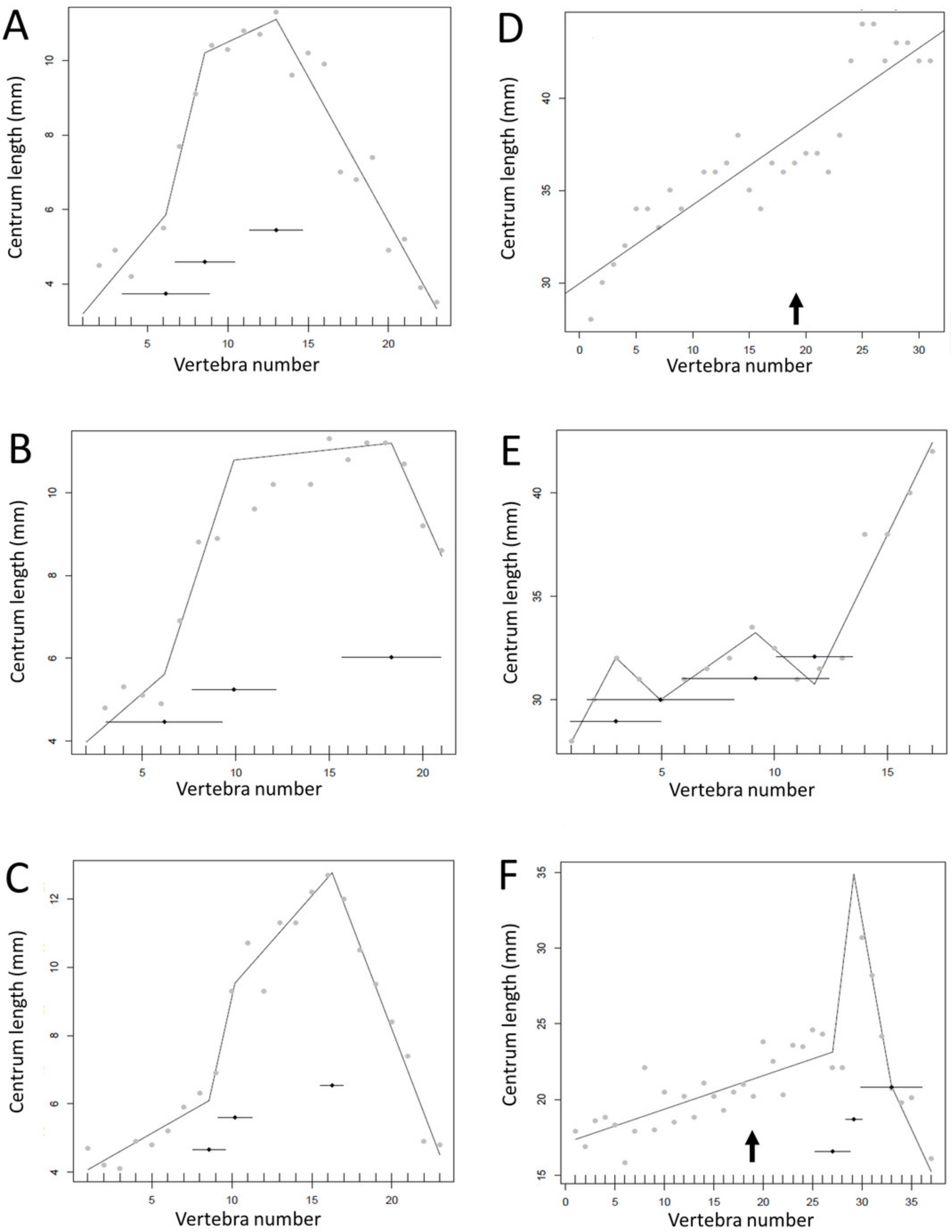

A
Centrum length (mm)
4
6
8
10
5
10
15
20
Vertebra number
D
Centrum length (mm)
30
35
40
0
5
10
15
20
25
30
Vertebra number
B
Centrum length (mm)
4
6
8
10
5
10
15
20
Vertebra number
E
Centrum length (mm)
30
35
40
5
10
15
Vertebra number
C
Centrum length (mm)
4
6
8
10
12
5
10
15
20
Vertebra number
F
Centrum length (mm)
15
20
25
30
35
0
5
10
15
20
25
30
35
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.

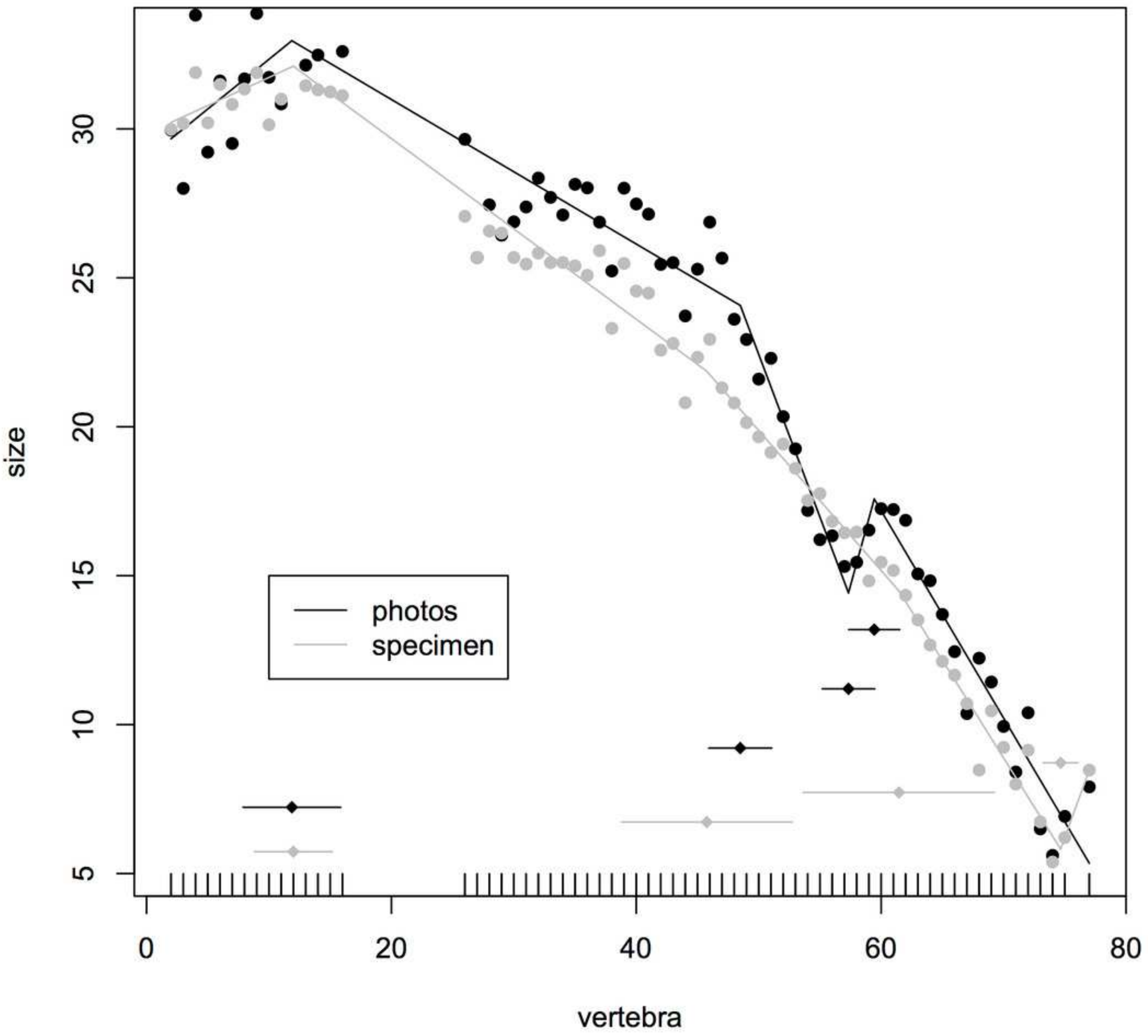

size
30
25
20
15
10
5
0
20
40
60
80
vertebra
photos
specimen

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).

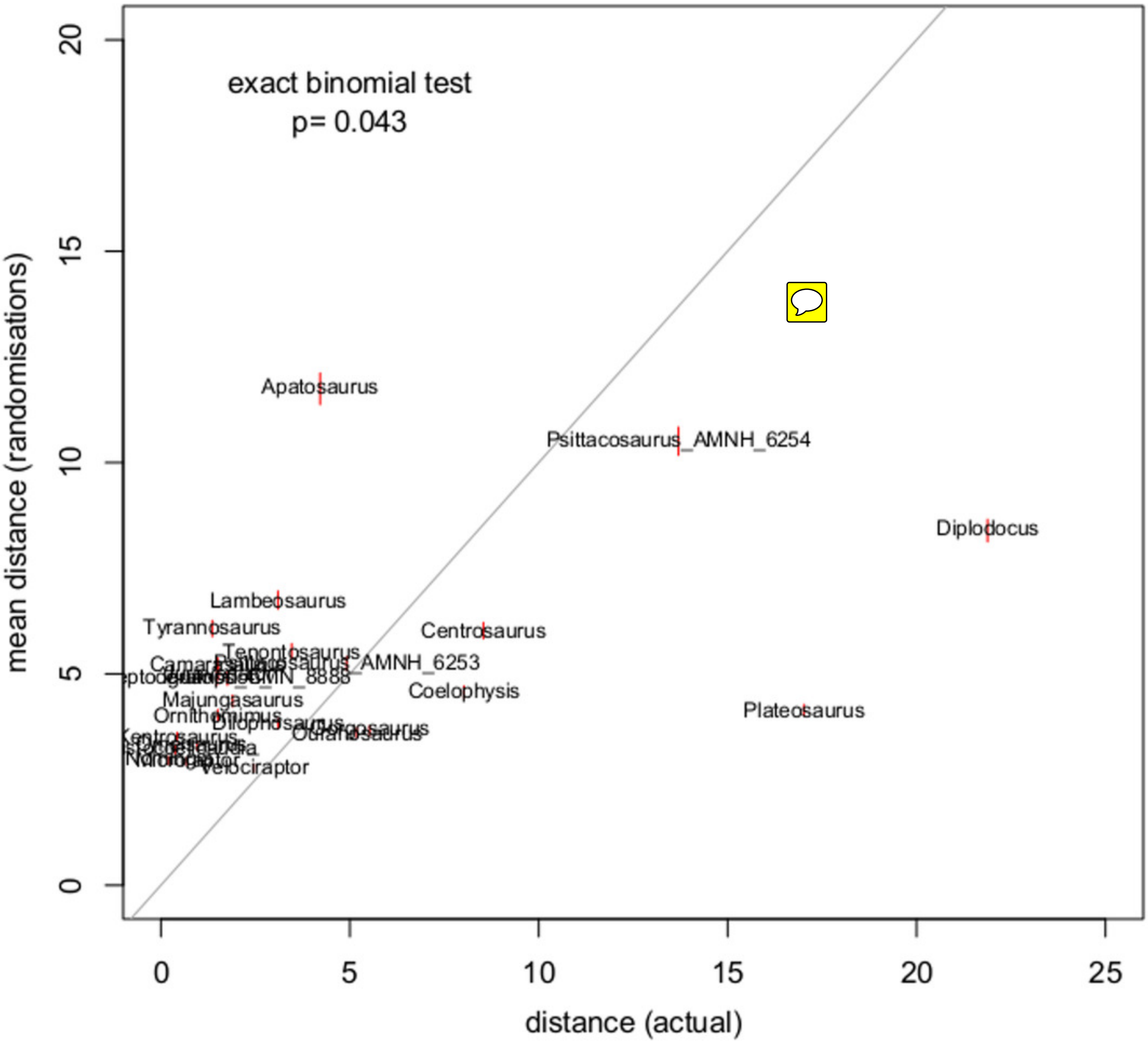

exact binomial test
p= 0.043
mean distance (randomisations)
distance (actual)
0
5
10
15
20
25
Apatosaurus
Psittacosaurus_AMNH_6254
Diplodocus
Lambeosaurus
Tyrannosaurus
Centrosaurus
Tenontosaurus
Camarasaurus
Psittacosaurus_AMNH_6253
_MN_8888
Coelophysis
Majungasaurus
Plateosaurus
Ornithomimus
Dilophosaurus
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.

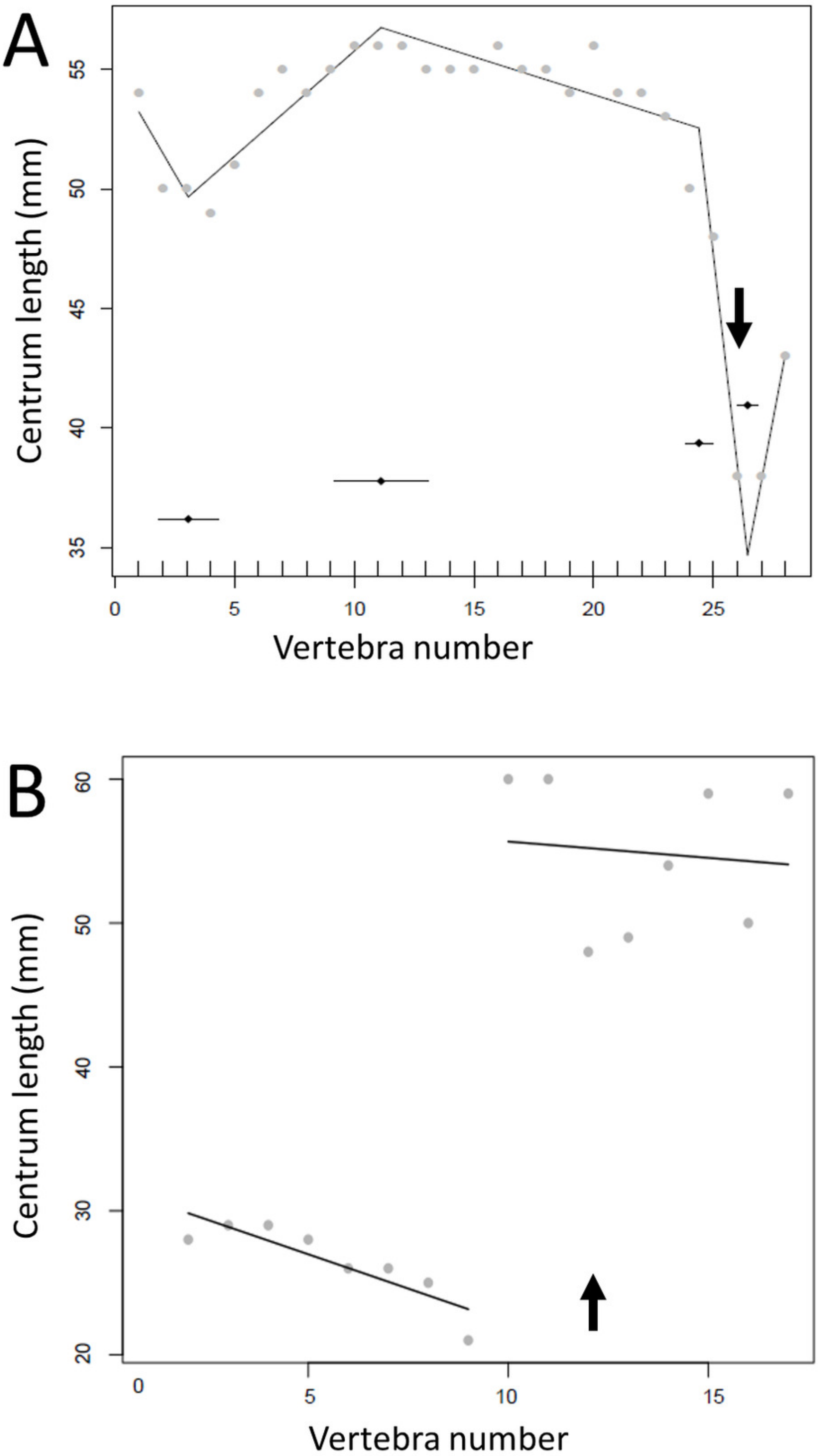

A
Centrum length (mm)
35
40
45
50
55
0
5
10
15
20
25
Vertebra number
B
Centrum length (mm)
20
30
40
50
60
0
5
10
15
Vertebra number

Figure 8

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

The stegosaur Kentrosaurus above, and ankylosaur Dyoplocephalus below.

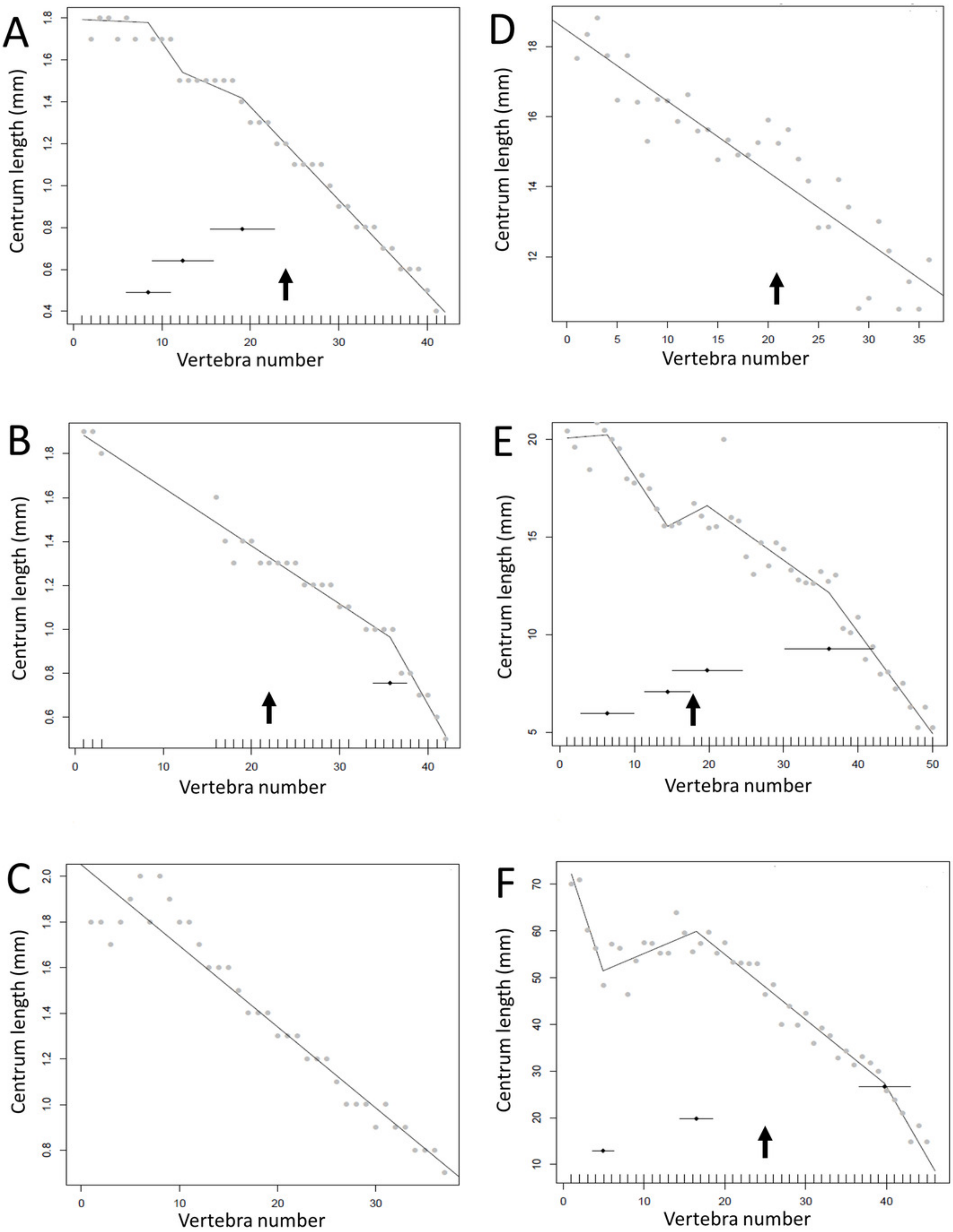

A
Centrum length (mm)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0
10
20
30
40
Vertebra number
D
Centrum length (mm)
18
16
14
12
0
5
10
15
20
25
30
35
Vertebra number
B
Centrum length (mm)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0
10
20
30
40
Vertebra number
E
Centrum length (mm)
20
15
10
5
0
10
20
30
40
50
Vertebra number
C
Centrum length (mm)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0
10
20
30
Vertebra number
F
Centrum length (mm)
70
60
50
40
30
20
10
0
10
20
30
40
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.

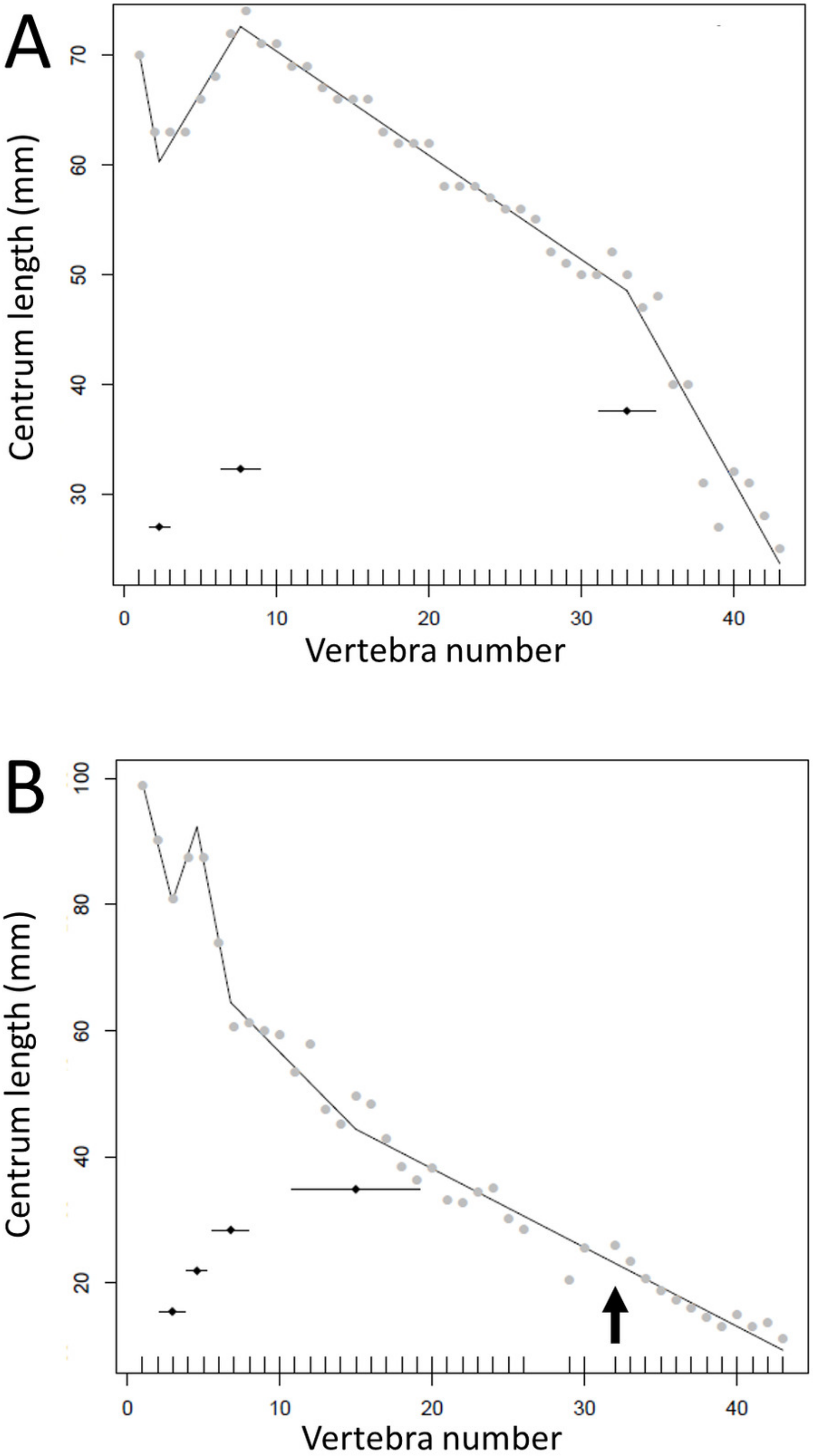

A
Centrum length (mm)
30
40
50
60
70
0
10
20
30
40
Vertebra number
B
Centrum length (mm)
20
40
60
80
100
0
10
20
30
40
Vertebra number

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.

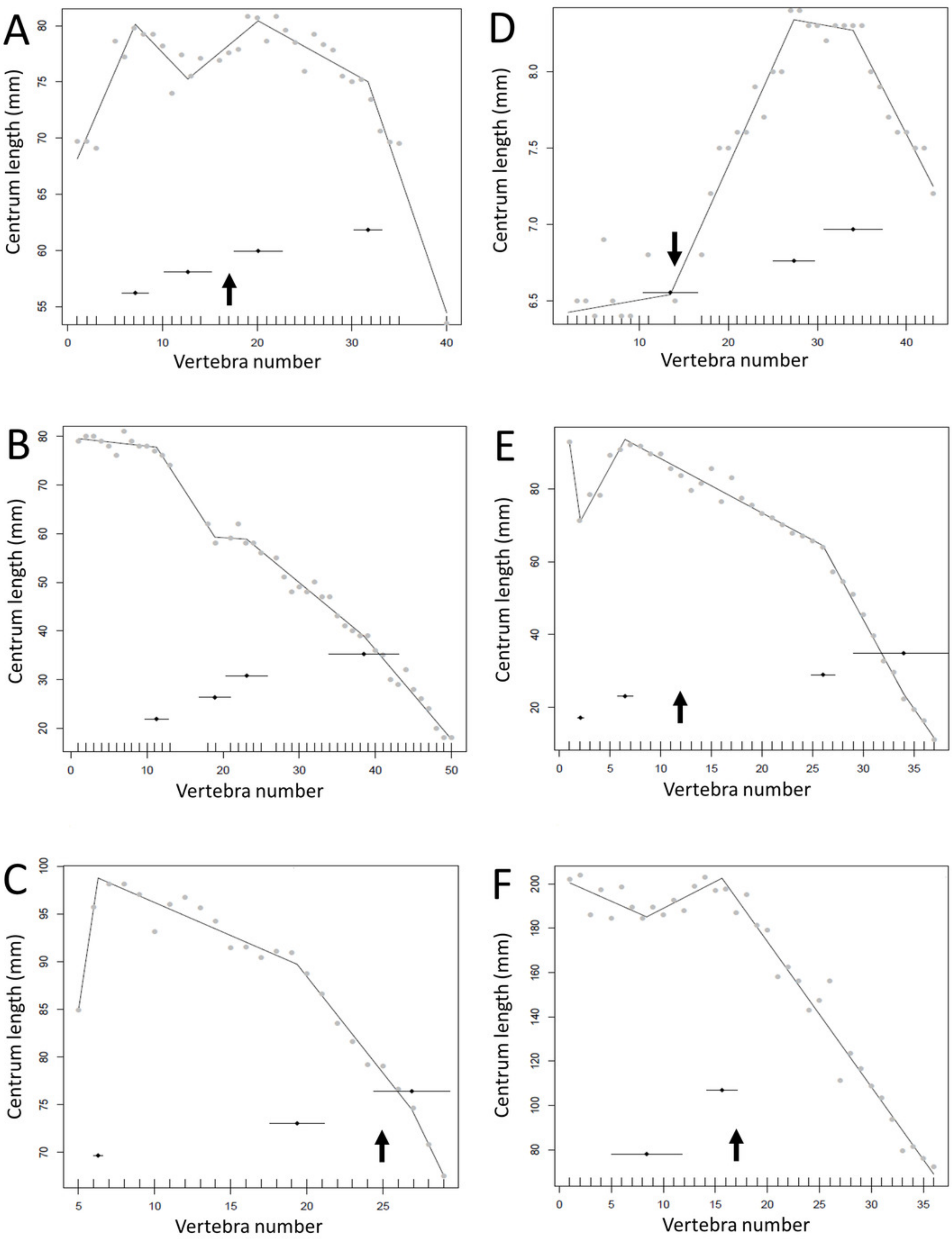

A
Centrum length (mm)
55
60
65
70
75
80
0
10
20
30
40
Vertebra number
D
Centrum length (mm)
6.5
7.0
7.5
8.0
10
20
30
40
Vertebra number
B
Centrum length (mm)
20
30
40
50
60
70
80
0
10
20
30
40
50
Vertebra number
E
Centrum length (mm)
20
40
60
80
0
5
10
15
20
25
30
35
Vertebra number
C
Centrum length (mm)
70
75
80
85
90
95
100
5
10
15
20
25
Vertebra number
F
Centrum length (mm)
80
100
120
140
160
180
200
0
5
10
15
20
25
30
35
Vertebra number

Figure 11

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

Centrum length patterns for non-maniraptoran theropods.

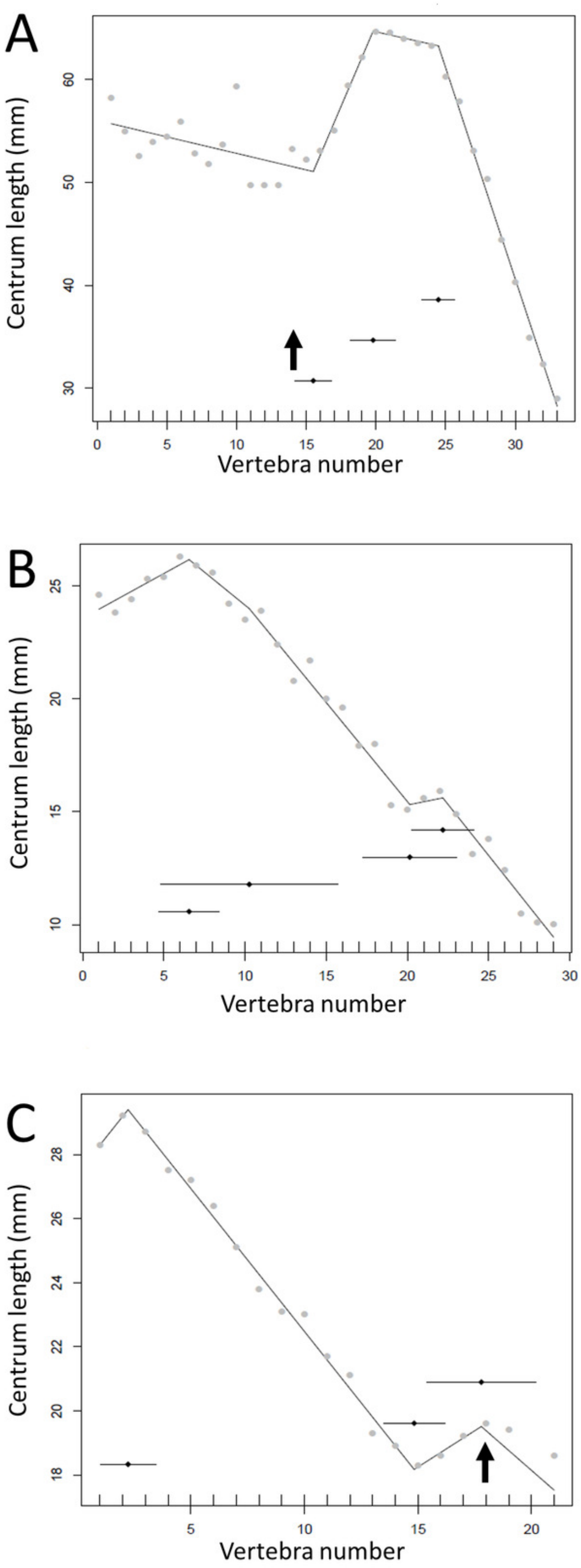

A
Centrum length (mm)
30
40
50
60
0
5
10
15
20
25
30
Vertebra number
B
Centrum length (mm)
10
15
20
25
0
5
10
15
20
25
30
Vertebra number
C
Centrum length (mm)
18
20
22
24
26
28
5
10
15
20
Vertebra number

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

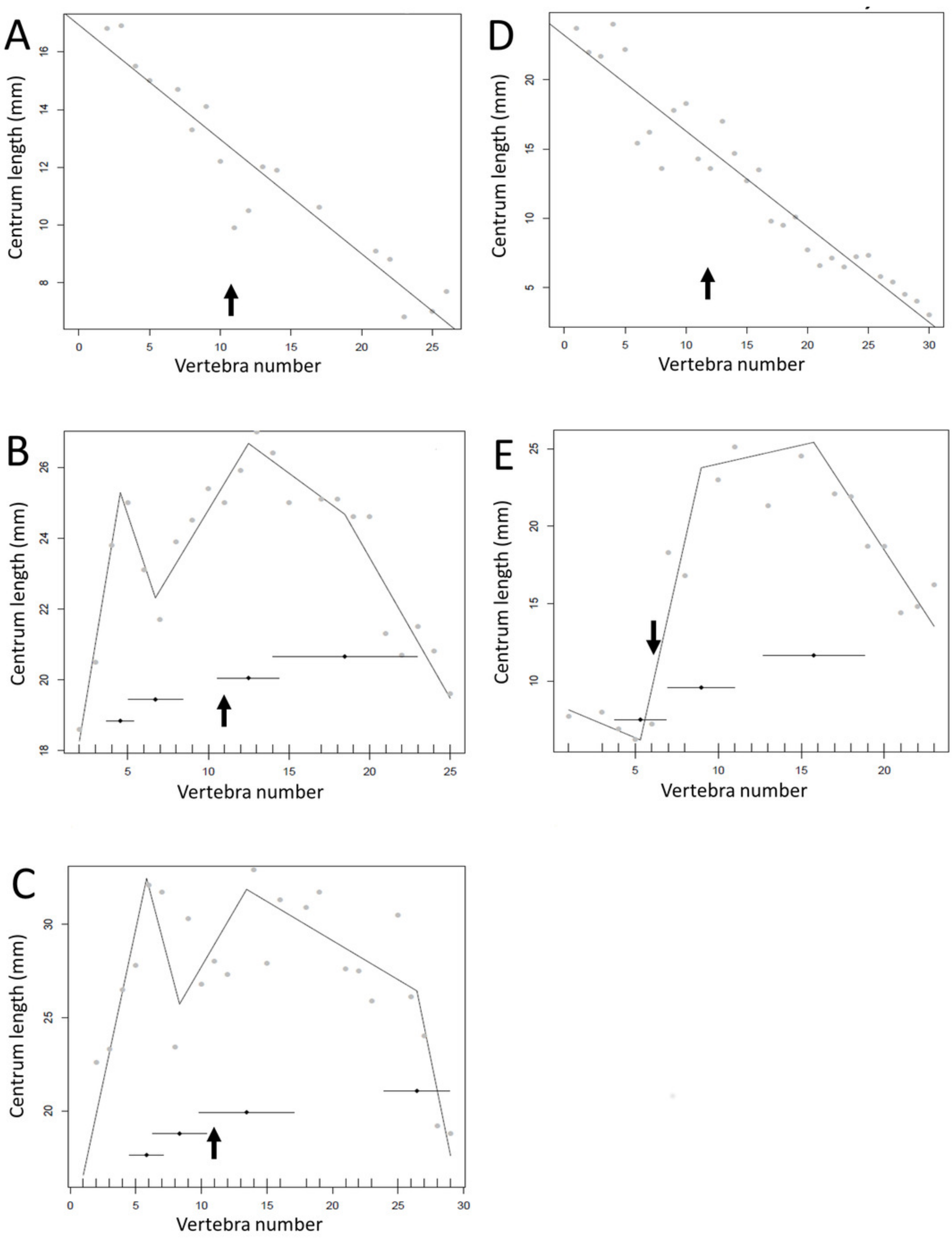
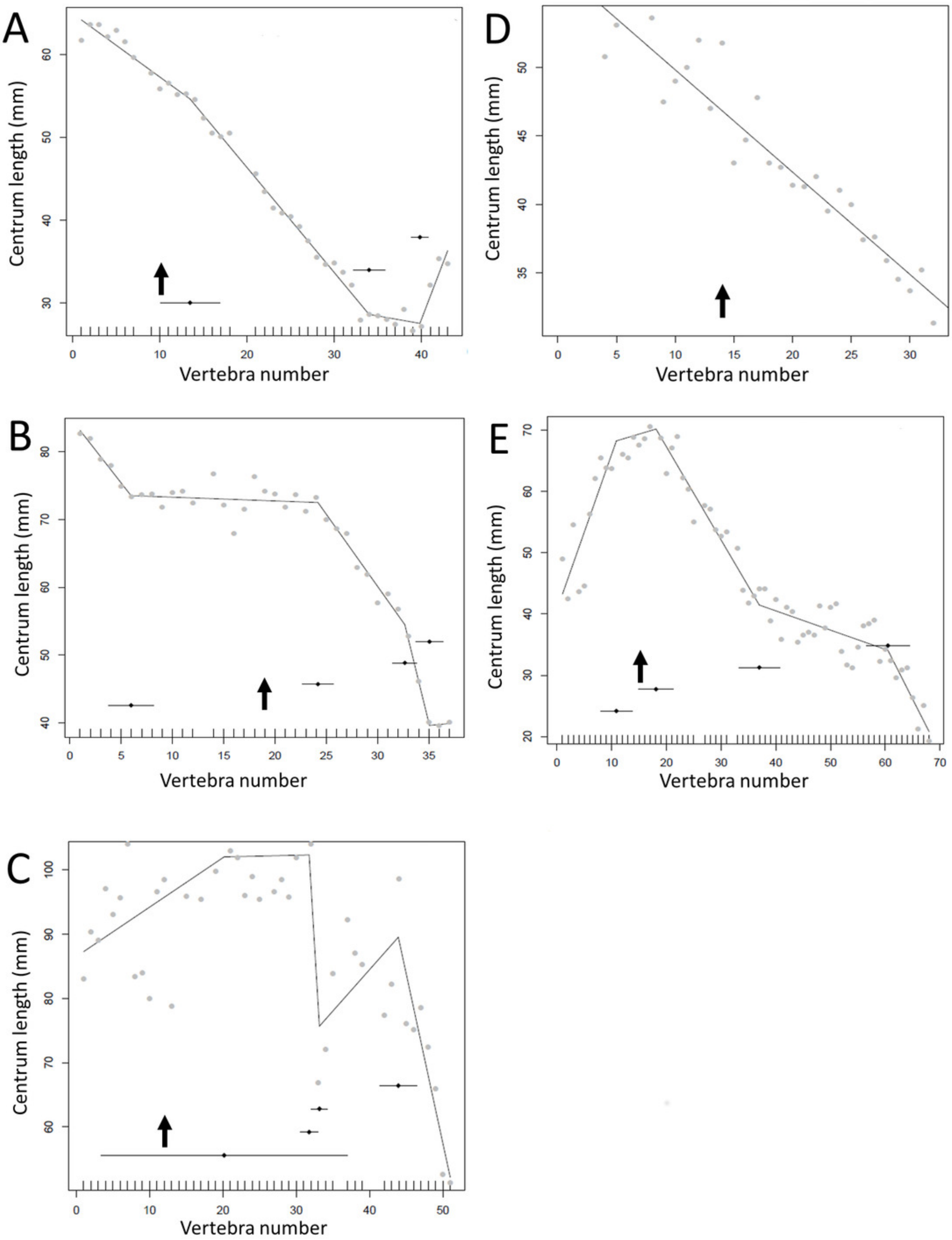

A
Centrum length (mm)
8
10
12
14
16
0
5
10
15
20
25
Vertebra number
B
Centrum length (mm)
18
20
22
24
26
5
10
15
20
25
Vertebra number
C
Centrum length (mm)
20
25
30
0
5
10
15
20
25
30
Vertebra number
D
Centrum length (mm)
5
10
15
20
0
5
10
15
20
25
30
Vertebra number
E
Centrum length (mm)
10
15
20
25
5
10
15
20
Vertebra number

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.


A
Centrum length (mm)
30
40
50
60
0
10
20
30
40
Vertebra number
D
Centrum length (mm)
35
40
45
50
0
5
10
15
20
25
30
Vertebra number
B
Centrum length (mm)
40
50
60
70
80
0
5
10
15
20
25
30
35
Vertebra number
E
Centrum length (mm)
20
30
40
50
60
70
0
10
20
30
40
50
60
70
Vertebra number
C
Centrum length (mm)
60
70
80
90
100
0
10
20
30
40
50
Vertebra number