

What do we mean by the directions “cranial” and “caudal” on a vertebra?

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Abstract

In illustrating vertebrae, it is important to consistently depict their orientation, so we can objectively assess and compare the slope of the neural arch, neural canal, or articular surfaces. However, differing vertebral shapes across taxa and across regions of the spinal column make it difficult to maintain consistency, or even define what we mean by the directions “cranial” and “caudal”. Consequently, characters such as “Neural arch slopes cranially 30° relative to the vertical” are disputable rather than objective measurements. Cranial and caudal are defined as directed along the horizontal axis, but several different definitions of “horizontal” are possible:

1. Long axis of centrum is horizontal. This is appealing for elongate vertebrae such as sauropod cervicals, but is not always well defined, and is difficult to determine for craniocaudally short vertebrae such as most caudals.

2. Articular surfaces of centrum are vertical. Difficult to determine when dealing with facets that are concave or (worse) convex; and ambiguous for “keystoned” vertebrae in which the facets are not parallel.

3. Neural canal is horizontal. Anatomically informative, but difficult to determine in vertebrae that have not been fully prepared or CT-scanned, and impossible to see in lateral view. Ambiguous for vertebrae where the dorsal and ventral margins of the canal are not straight or not parallel.

4. Similarity in articulation (“horizontal” is defined as a line joining the same point on two similarly oriented copies of the same vertebra when optimally articulated). This is less intuitive than definitions 1–3, but takes the entire vertebra into account.

We advocate explicitly stating a definition and using it consistently. In most cases, definition 3 (“Neural canal is horizontal”) best reflects anatomical and developmental realities, and it is therefore preferred. Low-tech methods can be used to determine neural canal orientation with adequate precision for most purposes.

Keywords: *vertebra, orientation, cranial, caudal, horizontal, neural canal*

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Introduction

In describing the vertebrae of animals, both extinct and extant, it is common to refer to characteristics such as “zygosphenal facets have their long axes inclined steeply anterodorsally” (Scanlon et al. 2003:594), “the neural arch slopes anteriorly from the posterior end of the centrum” (Blows 2014:237) and “the neural spine has now reverted to a more conventional posterior slope” (Norman 2020:65). In our own work, a diagnostic characteristic of the sauropod dinosaur *Xenoposeidon proneneukos* is “Neural arch slopes anteriorly 30°–35° relative to the vertical” (Taylor 2018a:5). But all of these characters can only be interpreted in light of a specific orientation of the vertebra in question. If the vertebra is pitched backwards 15°, a cranial slope of 35° becomes only 20° (Figure 1); and a cranial slope of 10° would become a caudal slope of 5°. Characters such as these may be used in a phylogenetic analysis, as for example C460 of Mannion et al. (2019), “Middle cervical neural spines, orientation of anterior margin in lateral view: vertical or sloping posterodorsally (0); anteriorly inclined (1)”. In such cases, the orientation in which the vertebra is examined can affect the scoring of a taxon, and potentially the tree topology recovered by the analysis. Orientation of vertebrae is therefore potentially crucial for descriptive purposes.

[Figure 1 here]

Beyond the simple need to measure angles of inclinations against an objectively defined baseline, there are biological questions for which we cannot give a well-defined answer except in

the context of a well-defined vertebral orientation. For example, although the spinal cord does not completely fill the neural canal in most vertebrates, the cross-sectional area of the neural canal does vary in concert with the cross-sectional area of the spinal cord. This allows us to estimate serial variation in spinal cord diameter, and to make inferences regarding gross patterns of limb use in extinct animals, including dinosaurs (Giffin 1990, 1992, 1995a, b). These estimates and inferences depend on the cross-sectional area of the neural canal — but the apparent area varies depending on how a vertebra is oriented when the measurement is taken. In most cases, sighting directly along the neural canal will maximize the apparent cross-sectional area of the neural canal as seen in cranial or caudal view. If the neural canal and articular surfaces of the centrum are not orthogonal, orienting the vertebra according to the verticality of the articular surfaces will result in a decreased apparent diameter of the neural canal (Figure 2).

[Figure 2 here]

For determining neural canal cross-section to estimate spinal cord size, we would prefer to orient the vertebra according to the long axis of the neural canal, as in Figure 2C–D. For other purposes, such as measuring the articular surface area of the centrum to estimate biomechanical loading or intervertebral cartilage properties, we might prefer to orient the vertebra with the articular surfaces vertical, as in Figure 2A–B. More generally, the complexity of vertebral geometry requires careful thought as to which definition of horizontality is appropriate in each analytical context.

In the present paper, we will propose and discuss four candidate criteria for defining horizontality, recommend the one we consider most practical and informative for most purposes, and show some practical techniques for determining horizontal orientation according to that criterion. In the absence of such criteria, it is inevitable that we will continue to see inconsistency such as that in our own (Taylor and Wedel 2013) illustration of the cervical vertebrae of a turkey and of *Giraffatitan brancai* (reproduced here as Figure 3).

[Figure 3 here]

We have been similarly inconsistent in our other papers, sometimes illustrating vertebrae with the neural canal horizontal even if that meant the centrum ends were tilted (e.g., Wedel and Taylor 2013: figure 7), but at other times illustrating vertebrae with the caudal articular surface vertical, even if that meant that the neural canal or centrum long axis was inclined (e.g., Wedel 2009: figure 7). Where we have been consistent, it has been through blind luck rather than careful consideration or deliberate choice: we did not perceive that there was a problem to be solved until the matter of orientation was raised in a review of Taylor’s (2018a) *Xenoposeidon* revision (see below).

Note that the present question is essentially a nomenclatural one. It has nothing to do with life posture, which is a much more difficult problem, subject to many more degrees of uncertainty, and so has no direct implications for biomechanics or functional morphology. Animals do not hold their vertebral columns at anything close to true horizontal (Taylor et al. 2009) — not even those that we usually characterize as having horizontal posture — and we do not want to tie the meaning of our very nomenclature to something so variable, unpredictable and behaviour-dependent. For example, in many birds, the cervical column is tightly S-curved so that the mid-cervical vertebrae are almost upside-down (Figure 4): we would certainly not want to define that habitual life posture as “horizontal” for the mid-cervicals.

[Figure 4 here]

Instead, we seek abstract notions of “horizontal”, “cranial” and “caudal” that apply irrespective of the specific posture adopted by an animal — something that is especially important for the study of extinct animals for which habitual posture cannot be known with certainty and remains controversial (e.g. sauropod neck posture: Stevens and Parrish 1999 vs. Taylor et al. 2009). Our goal is to have an objective standard by which to assess properties such as the slope of a neural arch.

Anatomical nomenclature

As dinosaur palaeontologists, we generally use and prefer the Owenian system of anatomical directions, with anterior and posterior indicating the forward and backward directions accordingly (Owen 1854) — hence the use of these terms in the *Xenoposeidon* paper, its reviews, and the associated discussion. However, for the present paper, we seek directional definitions that are appropriate and unambiguous for all vertebrates: not only those like dinosaurs, dogs and fish, which hold their vertebral columns essentially horizontal; but also those like humans, penguins and alert meerkats, which hold their vertebral columns essentially vertical. For this reason — avoiding ambiguity in humans, where “anterior” means ventral (towards the belly) rather than cranial (towards the head) — we will use the terms cranial and caudal. When the terms “anterior” and “posterior” appear in quoted material, they are always used in the Owenian sense that is equivalent to “cranial” and “caudal” respectively.

We use the abbreviation C_n to indicate the n th cervical vertebra.

In all lateral-view illustrations, vertebrae are illustrated as though in right lateral view, i.e. with the head towards the right. In some cases, that has necessitated reversing images of left-lateral views. In these cases, the reversal is noted in the image captions.

Although this paper appears in the *Journal of Paleontological Techniques*, the definitions proposed herein applies equally to the vertebrae of extant animals.

Institutional abbreviations

- **CM** — Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
- **FMNH** — Field Museum of Natural History, Chicago, Illinois, USA.
- **LACM** — Natural History Museum of Los Angeles County, Los Angeles, California, USA.
- **MB.R** — Museum für Naturkunde Berlin, Berlin, Germany; fossil reptile collection.
- **MWC** — Museum of Western Colorado, Fruita, Colorado, USA.
- **MNHAH** — Museum of Nature and Human Activities, Hyogo, Japan.
- **NHMUK PV** — Natural History Museum, London, UK; vertebrate palaeontology collection.
- **WRAZL** — The William R. Adams Zooarchaeology Laboratory, Indiana University Bloomington, Indiana, USA.
- **ZPAL** — Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Methods

Four definitions of “horizontal”

We have conceived four candidate definitions of what it might mean for a vertebra to be horizontal — and therefore what the directions cranial and caudal (and dorsal and ventral) might mean. We will now consider them in turn.

1. Long axis of centrum is horizontal

The default approach for most illustrations, especially for elongate vertebrae such as the cervicals of sauropods, pterosaurs, tanystropheids, giraffes and birds, has been to orient them more or less by eye. In practice, this means to draw a line between the cranial and caudal articular surfaces of the centrum at half height, and orient that line horizontally (Figure 5).

[Figure 5 here]

However, this approach cannot be meaningfully used for craniocaudally short vertebrae such as most caudals, in which there is no unambiguous long axis (Figure 6A).

And even for elongate vertebrae, this immediately intuitive approach breaks down when considered in detail. A line between the cranial and caudal articular surfaces at half height sounds simple, but to determine half-height we need to establish where the dorsal and ventral margins of the articular surfaces are, and this is not always clear, especially for fossil vertebrae. In Figure 5C, the upper blue lines at each end of the vertebra mark the dorsalmost extent of the two articular surfaces, and are not difficult to determine. But the ventralmost extent of both surfaces is much more ambiguous. Candidate ventral extents are shown by the other blue lines. Cranially (to the right), the ventralmost line is aligned with the ventralmost point on the cranial part of the vertebra, but it is not certain that this is part of the articular condyle rather than some other process; the two lines immediately above show two other points on the curvature of the condyle that could be interpreted as its ventralmost extent. The same problem is more extreme with respect to the ventral margin of the caudal articular surface (left side of Figure 5C). **Only with the benefit of a caudal view** does it become apparent that the upper two lines in the lower group mark breakages in the cotyle rim rather than a legitimate ventral margin, and that even the lowest line represents a point of breakage rather than for example, a separate ventrolateral process. In fact, the true ventral extent of this articular surface would have been located some way below the preserved portion of the bone — as is shown in Janensch’s (1950: figures 23, 25) illustrations of this vertebra and in Figure 5C.

All this shows that relying on the eye to determine horizontal orientation can be very misleading, and that a more objective approach is needed. We will now consider three such definitions (Figure 6).

[Figure 6 here]

2. Articular surfaces of centrum are vertical

In this approach, we define horizontal as that orientation in which the cranial and caudal articular surfaces of the centrum are vertical (Figure 6A, D). This is appealing when dealing with short, tall vertebrae, but less so for long, slender vertebrae such as the giraffe, turkey and *Giraffatitan*

cervicals of Figure 5.

For the *Haplocanthosaurus* caudal shown here, the current definition gives a nearly unambiguous result as the cranial and caudal articular surfaces are very close to parallel: in Figure 6A, where the green line showing the orientation of the caudal surface is vertical, the red line showing the orientation of the cranial surface is cranially inclined by less than one degree. However, its meaning is ambiguous for “keystoned” vertebrae in which the cranial and caudal surfaces are not parallel, as for example the giraffe C7 shown in Figure 6D, in which the caudal surface is inclined 19° more steeply than the cranial; or the *Sauroposeidon* C6 illustrated by Wedel and Cifelli (2005: figure 11A) in which the caudal surface is near vertical but the margin of the cranial condyle is inclined about 20°. (Note that in the former, the ventral surface is longer than the dorsal, but the converse is true in the latter.) “Keystoning”, while rarely as extreme as seen in these vertebrae, is extremely common, so when using Definition 2 it is necessary to specify which of the two articular surfaces is being used. Alternatively, an average articular-surface orientation could be used, such that in the “horizontal” orientation, the inclination of the cranial and caudal articular surfaces is equal and opposite.

Strongly opisthocoelous vertebrae such as giraffe cervicals, and strongly procoelous vertebrae such as monitor lizard caudals (Figure 7A) and crocodilian cervicals (Figure 7B) exemplify another difficulty of this definition: how does one even determine the orientation of an articular surface that is not flat? For concave surfaces such as the caudal articulation of the giraffe cervical and the cranial articulations of the monitor caudal and alligator cervicals, the best solution is probably to project a straight line between the cranialmost or caudalmost extremities of the dorsal and ventral surfaces, as shown by the green line in Figure 6D. However, these points are not always easy to determine: in the *Xenoposeidon* dorsal vertebra (Figure 1), the caudal margin of the neural arch appears in lateral view to blend into that of the centrum, so that there is no obvious point that is the caudalmost extremity of the dorsal surface of the centrum; and in the *Giraffatitan* cervical vertebra (Figure 5C), parts of the caudoventral margin of the vertebra are broken off, so it is not possible to determine the caudalmost extremity of the ventral surface. Convex surfaces such as the cranial articulation of the giraffe cervical and the caudal articulations of the monitor caudal and alligator cervicals present an even more difficult problem: what can be defined to be the orientation of a surface that is curved in lateral view? For some vertebrae, there is a clear ridge projecting outward from the concave articular extremity, and the orientation of that ridge can be used, as shown by the red line in Figure 6D. But this is not present in all opisthocoelous and procoelous vertebrae: and even when it is, the ridge is often somewhat ill-defined, so that superimposing an orientation line is more an art than a science.

[Figure G here]

Finally, the somewhat parallelogram-like shape of the giraffe C7 also illustrates yet another difficulty with this definition of horizontality: if the vertebra were oriented such that either the cranial (red line) or caudal (green line) articular surface were vertical, the resulting orientation, with a very obvious diagonal slope to the long axis of the vertebra, would immediately strike us as “wrong”. That in itself is not a fatal strike against the definition, but its violation of what strikes us intuitively as correct must weigh against it.

3. Neural canal is horizontal

The third definition fixed the orientation of the neural canal as “horizontal”, as shown in Figure 6B, E. For a given vertebra, this can yield extremely different results from Definition 2, as seen in the contrast between the two orientations shown of the *Haplocanthosaurus* caudal in parts A and B of Figure 6 and the giraffe cervical in parts D and E of figure 6. It can also be seen that the Komodo dragon caudal in Figure 7A, which is here depicted with the neural canal close to horizontal, would be oriented very differently according to Definition 2.

However, this definition, too, is subject to some ambiguity.

First, just as Definition 2 can yield a different orientation depending on whether the orientation of the cranial or caudal articular surface is used, so the present definition can yield a different orientation depending on whether the orientation of the roof or the floor of the neural canal is used: compare the green and red lines approximating the floor and roof of the *Haplocanthosaurus* caudal in Figure 6B. For a tubular neural canal of constant diameter, this problem does not arise, but not all neural canals are this regular, and “trumpet-shaped” canals can yield widely divergent orientations of roof and floor. For this reason, when using Definition 3, it is necessary to specify whether the roof or floor of the neural canal is being used. Alternatively, an average neural-canal-margin orientation could be used, such that in the “horizontal” orientation, the inclination of the roof and floor of the neural canal is equal and opposite. However, we do not recommend the use of an average, as it requires two potentially awkward measurements to be made, may not be possible with poorly preserved fossil vertebra, and introduces additional complexity.

A second difficulty, as again shown by the *Haplocanthosaurus* caudal of Figure 6A–C, the individual margins of the neural canal may not be straight. This is particularly apparent for the floor of the canal, which is deeply dishd. However, it is easy in this case to define the orientation of the neural canal floor as that of a straight line joining its cranialmost and caudalmost extent. A less obvious but more profound difficulty is presented by the roof of this vertebra’s neural canal, in which it is not apparent where the cranialmost point is: two equally credible alternatives, points *a* and *b*, yield “horizontal” lines whose inclinations differ by 3.8° (Figure 8).

[Figure 8 here]

Even worse, when one or both of the margins of the neural canal is convex in cross-section, there is no cranialmost or caudalmost margin, and therefore no straight line to project between them as for example in *Homo sapiens*: see Figure 9.

[Figure 9 here]

A further difficulty with this definition is that, unlike the articular surfaces, the neural canals of vertebrae can be difficult to examine and measure. In fossil vertebrae, they are frequently not prepared out of matrix. But even when a complete and completely prepared vertebra is available, a physical or virtual sagittal hemisection is required to fully depict and determine the neural canal trajectory, and this is only rarely available. (However, see below for some methods of determining approximate neural-canal orientations.)

4. Similarity in articulation

Definition 1 is based on the centrum of the vertebra; Definition 2 is based on the cranial and caudal articular surfaces; and Definition 3 is based on the neural canal. But is it possible to arrive at a definition that takes the whole vertebra into account?

[Figure 10 here]

The definition that we call “similarity in articulation” (Figure 10) does this. It consists of three steps as follows:

1. Depict the vertebra in any orientation. (It doesn’t matter which orientation is chosen at this stage, as it will be changed in step 3.) Add another copy of the same vertebra in the same orientation (Figure 10A).
2. without rotating either copy, move them into the relative position that gives the best articulation, based on both the centrum articulations and the zygapophyses (Figure 10B).
3. Rotate the articulated grouping of both copies into the orientation where they are at same height (Figure 10C). The resulting orientation is deemed to be horizontal according to this definition.

Note that this definition does not require two vertebrae: it uses two *copies* of the *same* vertebra to determine the orientation of that vertebra in isolation, and so does not require a preserved sequence of vertebrae in order to be used.

Figure 6C shows the result of applying this definition to the *Haplocanthosaurus* caudal. Figure 6F shows the result of applying it to a giraffe *Giraffa camelopardalis* FMNH 34426, cervical 7. Note that the intercentral joint in Figure 6F shows a strong divergence between the planes of the two articular surfaces: a “better” articulation might be achieved between the two copies of the vertebra if one were allowed to rotate relative to the other, but that would not yield a single orientation and so would violate the mechanism of Definition 4.

This definition of “horizontal” is less intuitive than definitions 1–3, but has some advantages. First, it can be determined for any more or less complete vertebra, irrespective of whether or not the articular faces are parallel or the neural canal is tubular. Second we may hope that, since it uses the whole shape of the vertebra, this definition is less vulnerable to yielding a distorted result when the vertebra is damaged. Third, it constrains subjectivity to a single well-defined judgement which can be reviewed and revised as needed: that of how the two similarly-oriented copies of the vertebra best articulate together.

On the other hand, it also suffers from some difficulties. As seen in Figure 6F, it is not really possible to satisfactorily articulate consecutive copies of a keystone vertebra in the same orientation. Similarly, the definition is not really appropriate for transitional vertebrae, which in life would have articulated with vertebrae very different in form from themselves. Most seriously, though, Definition 4 requires a fairly complete vertebra to be usable at all.

Practical approaches to determining horizontal orientation

It is relatively easy to determine horizontal orientation under Definitions 1 and 2 for most vertebrae, as they depend on externally visible parts; and horizontality under Definition 4 is assessed using a lateral-view image of the vertebra, which is typically easy to obtain. But Definition 3 (“neural canal is horizontal”) is often more difficult to apply since the canal is not

visible in lateral view. Orientation by this definition can best be achieved by the use of CT scans or lengthways physical sectioning, but these approaches are not always available. We have successfully used two low-tech methods.

The paper-roll method

When dealing with a vertebra from an extant animal, or a fully prepared fossil in which matrix has been removed from the neural canal, the trajectory of the canal can often be approximated using a roll of paper pushed through the neural canal (Figure 11).

[Figure 11 here]

This is a case where an unsophisticated method gives surprisingly informative and reliable results. As the rolled-up paper naturally uncoils, it fills as much of the space of the neural canal as possible, giving a good sense of the trajectory of both the roof and floor of the canal. In a “trumpet shaped” neural canal that is wider at one end than at the other, the paper uncurls further at the wider end, giving a visual indication of the variation in width. This can be seen to a minor degree in Figure 11E, in which the neural canal of cervical vertebra 7 in a juvenile giraffe is slightly taller cranially than it is caudally.

The toothpick method

The paper-roll method can often not be used with fossil vertebrae, as their neural canals are frequently left unprepared so that they are filled with matrix. This is the case, for example, with the *Xenoposeidon proneneukos* holotype dorsal vertebra NHMUK PV R2095. However, the use of another low-tech method can give us the result (Figure 12). We used Blu-Tack to attach two toothpicks to the cranial and caudal ends of the neural canal floor, and manipulated the toothpicks so that they formed a straight line. We then oriented the vertebra such that this straight line was horizontal, as indicated by a spirit level held parallel to it. Using this method we were able to determine from photos that when the floor of the neural canal is horizontal, the slope of the neural arch is about 29°: just outside the 30°–35° range specified as character 2 in the revised diagnosis of Taylor (2018a:5).

[Figure 12 here]

Results

Each of the candidate definitions of “horizontal” has appealing qualities, and indeed when the definitions were proposed to a community of professional and amateur scientists on our blog, all the definitions had adherents (comments to Taylor 2018b). No one definition can satisfy all desiderata.

Definition 1 (Long axis of centrum is horizontal) is perhaps the least satisfactory of the approaches presented here, as it is the most dependent on a judgement “by eye”. It is also not readily applicable at all to craniocaudally short vertebrae.

While Definition 2 (articular surfaces of centrum are vertical) is perhaps the most frequently used orientation when illustrating craniocaudally short vertebra, it has the undesirable property that when a sequence of consecutive vertebrae are horizontally aligned in this orientation, the neural canal can be jagged (Figure 13).

[Figure 13 here]

This never happens in life: the spinal cord can curve but never kink: see for example Figure 14.

[Figure 14 here]

This jagged appearance could be avoided by illustrating the consecutive vertebrae at different heights, arranged like the steps of a staircase, but a definition of “horizontal” in which an articulated column of horizontal vertebrae cannot be drawn horizontally is not ideal.

By contrast, Definition 3 (“neural canal is horizontal”) is anatomically informative, corresponding to the reality of how consecutive vertebrae articulate in life, and to how they originate. Vertebrae may be found in isolation (e.g., NHMUK PV R2095, Figure 1), but they do not develop in isolation. Early in the embryological development of vertebrates, the notochord is the primary body axis, defining not only craniocaudal orientation but also dorsoventral and left–right (Stemple 2005 and references therein). The notochord induces the formation of the neural plate, which rolls up to become the neural tube, and eventually the brain and spinal cord (Spemann and Mangold 1924). From that point forward, the spinal cord lies dorsal to — and parallel to — the notochord, and then to the articulated vertebral centra that replace the notochord. In some vertebrae, the intervertebral joints form orthogonal to the notochord axis, so that the trajectory of the notochord can be reconstructed from the vertebral centrum. As we have demonstrated, however, in other vertebrae the intervertebral joints are not orthogonal to the notochord axis on which the vertebral column is patterned. If the long axis of the centrum is difficult or impossible to define, and if the intervertebral joints are not orthogonal to the trajectory of the vertebral column, then the only aspect of a vertebra that faithfully preserves the original axis of the parallel notochord and spinal cord is the neural canal. In such cases the geometry of the centrum’s articular surfaces is actively misleading with respect to the original notochordal/vertebral axis.

There is some precedent in the literature for the use of Definition 3. In Tschopp et al.’s (2015) specimen-level analysis of diplodocids, the brief discussion of Character 194 (cranial extent of prezygapophyses, page 94), the authors note that “The neural canal should be held horizontally, in order to accurately assess the expansion of the prezygapophysis”. Orientation by neural canal is also used in illustration such as that of caudals 6–8 of the *Opisthocoelicaudia skarzynskii* holotype ZPAL MgD-I/48 in Borsuk-Bialynicka (1977: plate 5: figure 2a), but in such cases this was not necessarily a choice consciously made by the author. In the case of *Opisthocoelicaudia* caudals, the three vertebrae were preserved in articulation in this orientation, suggesting that in this case as in most, this was the relative orientation in life.

Definition 4 (similarity in articulation) was initially appealing because it takes the whole vertebra into account, rather than only the articular surfaces of the centrum (as in Definition 2) or only the neural canal (as in Definition 3). In practice, however, this means that the definition cannot be used at all unless the vertebra is sufficiently well preserved to have well-formed articular surfaces both at the centrum and at the pre- and post-zygapophyses. This rules out its use for many fossil vertebrae — including NHMUK PV R2095, the *Xenoposeidon proneneukos* holotype dorsal vertebra which was the catalyst for this whole project. We are therefore not able to recommend the use of this definition, at least not when dealing with fossils.

Discussion

Recommendations

In discussing the angles of inclination of parts of vertebrae, it is essential to have a rigorously defined baseline: a concept of what is meant by the directions cranial and caudal, and therefore what axis is defined as horizontal, and therefore what is vertical. In this paper, we have proposed four candidate definitions. At minimum, we advocate that each paper that discusses vertebral shape and the inclination of parts should explicitly adopt some specific definition of “horizontal”, and use it consistently.

We recommend that the neural-canal-is-horizontal definition should be used in most cases, for the following reasons:

- It is well defined for both long and short vertebrae.
- It corresponds to the physical reality of the unkinked spinal cord.
- It reflects the developmental reality of how vertebra are formed.
- It can be used when only a relatively small part of the vertebra to be preserved.

When the floor and roof of the neural canal are not parallel, we generally recommend using the floor, both because it more nearly follows the embryonic notochord and because it is preserved in partial vertebrae in which the neural arch is lost — a more common condition than the loss of the centrum with the arch preserved. In these rarer cases, the roof of the canal must of course be used instead.

Implications for taxonomic characters

The genesis of the present paper was in late 2017, when one of us submitted a paper (Taylor 2018a) redescribing the sauropod dinosaur *Xenoposeidon* and assigning it to the group Rebbachisauridae, based on the holotype and only specimen NHMUK PV R2095. Among the five diagnostic characters that the manuscript gave for *Xenoposeidon* was #2, “Neural arch slopes anteriorly 35° relative to the vertical”. In two helpful and detailed rounds of peer review, Phil Mannion (2018a, 2018b) commented:

The strong anterior slant of the neural arch appears to be dependent on how you’ve chosen to orientate the vertebra, but there doesn’t appear to be any need to orientate it in this way.

[...]

I went into the NHM to re-look at this. No aspect of the posterior articular surface of the centrum leads me to orient the vertebra in the same way of shown in your figures. In addition, as currently orientated, the floor of the neural canal is strongly tilted — it seems more conservative to assume that this is horizontal. Similarly, by following that orientation, this would then make the long-axis of the lateral pneumatic opening closer to horizontal. By orientating the vertebra this way, the anterior margin is sub-vertical, with a very gentle anterior deflection (i.e. fairly normal for a sauropod), and the M-lamina is much closer in orientation to that of *Rebbachisaurus*.

After publication of the paper, the question Mannion had raised continued to play on the minds

of both present authors: what exactly *is* the “correct” orientation of the vertebra, relative to which we can measure the angle of the sloping neural arch? Figure 1 shows the difference between the slope as published (part A), and as interpreted by Mannion (part B).

In light of the recommendations of the present paper, we reoriented the *Xenoposeidon* vertebra according to Definition 3 (floor of neural canal is horizontal). As noted above, we used the toothpick method to determine that when the floor of the neural canal is horizontal, the slope of the neural arch is about 29°. We therefore recognize that Mannion (2018a, 2018b) was to some degree correct that the orientation depicted by Taylor and Naish (2007) and Taylor (2018a) was not horizontal and that the slope was therefore exaggerated (according to Definition 3). However, the initially stated slope of 35° was exaggerated only by 6° rather than the 15° suggested by Mannion’s (2018a) recommendation of a “sub-vertical” cranial margin. The slope of 30°–35° stated in the final published version of the paper (Taylor 2018a:5) is a better representation of the true morphology when using the neural canal as the determinant of horizontality.

This re-evaluation was potentially significant in interpreting NHMUK PV R2095: the forward slope of the neural arch is an important diagnostic character (as well as being the source of the species name *proneneukos*, “forward sloping”). Had Mannion’s preferred orientation been adopted, the forward slope would not be sufficiently strong to warrant a diagnostic role, and the validity of the taxon would have been undermined. It is similarly important to use a consistent orientation when scoring taxa for slope-related phylogenetic characters like C460 of Mannion et al. (2019)’s analysis.

Open peer review

In publishing the *Xenoposeidon* revision (Taylor 2018a) in the journal *PeerJ*, I (Taylor) was pleased to take advantage of the journal’s policy of allowing submitted drafts, peer-reviews, response letters and handling editors’ comments to be published alongside the final paper. It is because these materials are published (Young et al. 2018) that the sequence of discussion is preserved, and Mannion’s helpful and gracious comments on vertebral orientation are available to be read — not only as the extracts in the present paper, but in their full context.

We endorse the publication of peer reviews, and both take this option whenever it is offered. Aside from their value as part of the scholarly record, published peer-reviews are visible evidence of the reviewers’ broader contribution to science, and can be taken into account in evaluating researchers for jobs, promotions, tenure and grants. Sets of reviews, accompanied by the corresponding versions of the manuscript, can be an important pedagogical tool for teaching students in practical terms how peer-review works: for example, Andy Farke (Raymond M. Alf Museum) writes “I use those published reviews when we are talking about the process of scientific publication. I have the students read the reviews and read the responses, and then talk about how the paper changed as a result” (pers. comm. 2018). Crucially, reviews can also play an important role in the origination of new research questions, and should be acknowledged: the present work on defining vertebral orientation arises directly from Phil Mannion’s peer-review comments (Mannion 2018a, 2018b).

Acknowledgements

First, we thank Phil Mannion (Imperial College London) both for his multiple rounds of review of the *Xenoposeidon* manuscript and for giving us permission to quote relevant excerpts in the current paper. We also thank Marc Vincent for permission to reproduce his photograph in Figure 4 Jess Miller-Camp for responding to a cry for help on Twitter and providing the alligator cervical photograph in Figure 7, and Andy Farke for permission to cite a personal communication.

We thank John Hutchinson (Royal Veterinary College, UK) for supplying the juvenile giraffe neck from which we prepared the vertebrae used in Figure 11D–E, and Matt Cobley (Judge Memorial Catholic High School, Salt Lake City, UT) for the ostrich neck skeleton whose vertebra appears in Figure 11F.

We are deeply grateful to the curators and collection managers for access to specimens used in this study, including:

- Daniela Schwarz (Museum für Naturkunde Berlin) for *Giraffatitan*.
- Julia McHugh (Dinosaur Journey) for *Haplocanthosaurus*.
- Bill Simpson (Field Museum of Natural History, Chicago, IL) for *Brachiosaurus* and the mature giraffe.
- Neftali Camacho (Los Angeles County Museum of Natural History) for the Komodo dragon.
- Sandra Chapman (Natural History Museum, London, UK) for *Xenoposeidon*.
- Ken Noriega (Western University of Health Sciences) for the horse head.

We thank John Yasmer and Thierra Nalley (Western University of Health Sciences) for their assistance in CT scanning and 3D modelling the *Haplocanthosaurus* caudal vertebra.

Ryan D. Marek, Emanuel Tschopp and Peter Falkingham provided valuable reviews on an earlier version of this manuscript that helped it towards its present structure.

This work first began to take shape as a series of blog-posts (Taylor 2018b, Taylor 2018c, Wedel 2018a, Wedel 2018b, Wedel 2018c) which were drawn together in a talk (Taylor and Wedel 2018) presented by Taylor as part of the 1st Palaeontological Virtual Congress (<http://palaeovc.uv.es/>) and announced online (Wedel 2018d). Once work began on the manuscript, this was open to be read and commented on (Taylor 2018d). We commend this approach as valuable for soliciting informal feedback early in the process, and in making the research itself available quickly.

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Figure Captions

Figure 1. NHMUK PV R2095, the holotype dorsal vertebra of *Xenoposeidon proneneukos* in left lateral view (reversed). **A.** In the canonical orientation that has been used in illustrations in published papers (Taylor and Naish 2007, Taylor 2018a). **B.** Rotated 15° “backwards” (i.e. anticlockwise in this reversed view, with the dorsal portion displaced caudally), yielding a sub-vertical cranial margin in accordance with the recommendation of Mannion (2018b). In both parts, the blue line indicates the horizontal axis, the green line indicates the vertical axis, and the red line indicates the slope of the neural arch as in Taylor (2018a: figure 3B, label 2). In part A, the slope (i.e. the angle between the red and green lines) is 35°; in part B, it is 20°.

Figure 2. Varying apparent cross-sectional area of the neural canal of *Haplocanthosaurus* sp. MWC 8028, caudal vertebra ?3, depending on the orientation of a vertebra. **A and C.** Right lateral view in two different orientations. **B and D.** Cranial views in the same two different orientations. Parts **A** and **B** depict the vertebra oriented according to Definition 2 (articular surfaces of centrum are vertical), and show a neural canal that appears relatively small (5870 pixels) in cross-sectional area; parts **C** and **D** depict the vertebra oriented according to Definition 3 (neural canal is horizontal), and show a neural canal that appears 61% larger (9458 pixels) in cross-sectional area.

Figure 3. Inconsistent vertebral orientation in our own work (Taylor and Wedel 2013: figure 2). Representative mid-cervical vertebrae from a turkey (top) and the sauropod *Giraffatitan brancai* (bottom), not to scale. Each vertebra is shown in left lateral view (on the left) and caudal view (on the right). Articular surfaces, where each vertebra meets its neighbour, are highlighted in red (for the centra) and blue (for the zygapophyses). Articular surfaces that are concealed from view are cross-hatched: prezygapophyses face upwards and inwards, so that the facets are inclined towards the midline. In sauropods, the centra have ball-and-socket joints. In birds, the joints are saddle-shaped, and the cranial articular surface is hidden in lateral view. Note that the turkey vertebra is illustrated with the long axis of the centrum horizontal (Definition 1) even though this makes the articular surfaces non-vertical; while the *Giraffatitan* vertebra is illustrated with the caudal articular surface vertical (Definition 2) even though this causes the long axis of the centrum to be inclined. Reproduced under the CC By license.

Figure 4. Parrot skeleton with hemisected integument (probably *Amazona ochrocephala*) in left lateral view (reversed), in the Natuurhistorisch Museum of Rotterdam. Photograph by Marc Vincent, used with permission. Note the very strong S-curve of the neck, such that the most caudal cervical vertebrae are inclined downwards, then more cranial vertebrae are, progressively, inclined upwards, near vertical, sloping *backwards*, then vertical again, and finally sloping upwards to the skull.

Figure 5. Long cervical vertebrae oriented by Definition 1 (long axis of centrum is horizontal). **A.** Giraffe *Giraffa camelopardalis angolensis* FMNH 34426, 3rd cervical vertebra in left lateral view (reversed). **B.** Domestic turkey *Meleagris gallopavo domesticus*, 7th cervical vertebra in left lateral view (reversed). **C.** *Giraffatitan brancai* lectotype MB.R.2180 (formerly HMN SI), 5th cervical vertebra in right lateral view. All vertebrae are oriented horizontally according to the long axis of the vertebra (long red line). The long axis may be

defined as the line between the vertical midpoints of the cranial and caudal articular surfaces — but the heights of those midpoints depend on the selection of dorsal and ventral extremities of those surfaces, and these are not always obvious, especially in fossils, which are prone to damage. In part C, the short blue lines at each end of the vertebra show candidate margins. At both cranial and caudal surfaces, the dorsal margin is more or less uncontroversial; but there are several candidates for the ventral margin, especially for the caudal articular surface. These are impossible to resolve using only lateral-view photos and potentially even with the complete fossil to hand. The grey outline and shaded area at the caudoventral extremity of the vertebra shows a reconstruction of the undamaged shape of the cotyle, based on Janensch’s (1950: figure 23) drawing — which in turn may have been based on the bone itself in a better state of preservation than currently pertains, or may have been speculative based on the specimen more or less as it is now.

Figure 6. Orientation Definitions 2–4 illustrated for the two vertebrae. **A–C**, 3D digital model of *Haplocanthosaurus* sp. MWC 8028, caudal vertebra ?3, in cross section, showing medial aspect of left side, with cranial to the right; **D–F**, Giraffe *Giraffa camelopardalis* FMNH 34426, cervical 7 in left lateral view (reversed). **A, C**. In “articular surfaces vertical” orientation (Definition 2). The green line joins the dorsal and ventral margins of the caudal articular surface, and is oriented vertically; the red line joins the dorsal and ventral margins of the cranial articular surface, and is close to but not exactly vertical, inclining slightly forwards in *Haplocanthosaurus* vertebra and more strongly backwards in the giraffe vertebra. **B, E**. In “neural canal horizontal” orientation (Definition 3). The green line joins the cranial and caudal margins of the floor of the neural canal, and is oriented horizontally; some guesswork is required in the case of the giraffe, as only a lateral-view photograph is available. The red line joins the cranial and caudal margins of the roof of the neural canal in the *Haplocanthosaurus* vertebra (but see Figure 8), and is close to horizontal but inclined upwards; no similar line can be attempted in the giraffe. **C, F**. In “similarity in articulation” orientation (Definition 4). Two copies of the same vertebra, held in the same orientation, are digitally articulated optimally, then the pair is rotated as a unit until the two are level. The green line connects two copies of the same point on each copy of the vertebra, and is horizontal. For the *Haplocanthosaurus* vertebra, the uppermost point of the prezygapophyseal rami are used, and for the giraffe vertebra, the lowest point of the parapophyses is used; but a horizontal line could join the two copies of any point. It happens that for both these vertebrae Definitions 3 and 4 (parts B and C, and parts E and F of this illustration) give very similar results, but this is accidental. The 7th cervical vertebra of the giraffe is strongly “keystoned”, with the centrum (excluding the articular condyle) forming a parallelogram whose dorsal length is less than its ventral length. The angle between vertical green line and red “nearly vertical” line in part D is about 19°, meaning that if the two copies of the vertebra were oriented such that the cranial and caudal articular surfaces were optimally articulated, there would be a 19° angle between the vertebrae.

Figure 7. Procoelous vertebrae for which it is difficult to determine the orientation of the articular surfaces, depicted not to scale but with the same vertebral height. **A**. Komodo dragon *Varanus komodoensis*, LACM Herpetology specimen 121971, proximal caudal vertebra in right lateral view. Note the extremely convex and strongly inclined caudal articular surface to the left; the cranial articular surface to the right is correspondingly concave and almost as

strongly inclined. **B.** *Alligator mississippiensis* WRAZL 9840044, seventh cervical vertebra (with cervical rib attached) and sixth cervical vertebra (without rib) in articulation, in right lateral view. Photograph kindly provided by Jess Miller-Camp. While the caudal articular surfaces are strongly convex, the orientation of each can be interpreted as that of the well-defined “collar” that surrounds it.

Figure 8. 3D digital model of *Haplocanthosaurus* sp. MWC 8028, caudal vertebra ?3, in cross section, showing the ambiguous interpretation of the roof of the neural canal. **A.** The vertebra oriented according to a long interpretation of neural canal extent. The vertical blue line indicates the position identified as the cranialmost extent of the roof of the neural canal (point *a*), and the red line shows the interpretation of “horizontal” based on that location. **B.** The same vertebra, but with a different choice of cranialmost extent of the roof of the neural canal (point *b*), again marked with a vertical blue line. When a line is projected from here to the same caudalmost extent as in part A, the resulting notion of “horizontal” differs by 3.8°.

Figure 9. Right halves of two vertebrae from the lumbar (caudal dorsal) region of a human *Homo sapiens* in sagittal cross-section (cranial to left). Modified from Gray (1858: figure 99). Pale yellow indicates bone in cross-section, grey indicates both bone further from the midline and soft tissue. The red lines mark the floor of the neural canal: since the cranial and caudal ends of the floor of the canal are slightly elevated dorsally relative to the middle part of the canal, it is easy to project a line between these eminences and designate this as the trajectory of the canal. The blue lines mark the roof of the neural canal, but this is convex throughout its length for each vertebra. There is therefore no way to designate any single tangent to it as the trajectory of the neural canal roof of the vertebra as a whole.

Figure 10. The steps of the similarity-in-articulation method of determining horizontal orientation of a vertebra (Definition 4), illustrated using 3D digital model of *Haplocanthosaurus* sp. MWC 8028, caudal vertebra ?3. **A.** Two identical copies of the same vertebra depicted in the same orientation. **B.** The two copies brought into the best whole-vertebra articulation that can be achieved without rotating either. **C.** The articulated pair rotated together into that orientation in which they are at the same height. This orientation is designated as horizontal according to the present definition.

Figure 11. A selection of vertebrae with the approximate trajectory of their neural canals determined by the simple method of pushing a rolled-up piece of paper through their neural canals. **A.** *Brachiosaurus altithorax* holotype FMNH P 25107, first and partial second caudal vertebrae in right lateral view. **B.** *Camarasaurus* sp. CM 584, proximal caudal vertebra ?4 in right lateral view. **C.** *Camarasaurus* sp. CM 584, mid-caudal vertebra ?12 in left lateral view (reversed). **D.** Juvenile giraffe *Giraffa camelopardalis*, cervical vertebra 6 in left lateral view (reversed). **E.** Juvenile giraffe *Giraffa camelopardalis*, cervical vertebra 7 in left lateral view (reversed). Note the much stronger inclination than in C6, and that the neural canal is slightly “trumpet shaped”, being taller cranially than caudally. **F.** Ostrich *Struthio camelus*, cervical vertebra 16 in left lateral view (reversed).

Figure 12. 3D print of the *Xenoposeidon proneneukos* holotype dorsal vertebra NHMUK PV R2095, oriented horizontally according to Definition 3 (neural canal is horizontal) by the toothpick method. From left to right: left caudolateral (reversed), left lateral (reversed) and

left craniolateral (reversed) views. The camera is at the same level as the floor of the neural canal, so that the toothpicks appear horizontal in the oblique views as well as in the lateral view. The oblique views show that the toothpicks are located at the base of each end of the neural canal, and the horizontal view shows that the two toothpicks are aligned. This procedure was carried out using a 3D print of the vertebra from the scan data published as the supplementary file to Taylor (2018a), as the fossil itself was not readily available.

Figure 13. Two consecutive instances of hemisected 9th cervical vertebra of a domestic turkey, *Meleagris gallopavo domesticus*, in right medial view, oriented according to Definition 2 (red lines show vertical orientation of the caudal articular surface) and aligned horizontally. Since the orientation of the neural canal in this vertebra is inclined about 15° to perpendicular with the caudal articular surface, the result is a kinked spinal cord (shown in green) — something that never happens in life.

Figure 14. Sagittally bisected head and cranial neck of a horse *Equus ferus caballus* in left medial view (reversed). Of the cervical vertebrae (highlighted in red), the first four are complete but only the cranial part of the fifth is present. Note that the neural canal (highlighted in blue) runs in a nearly straight line, and is not kinked.