EXTANT ANIMALS PROVIDE NEW INSIGHTS ON HEAD AND NECK POSTURE IN SAUROPODS

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SAUROPOD NECK POSTURE REMAINS CONTENTIOUS

The habitual neck posture of sauropod dinosaurs has been controversial for as long as their body-plan has been understood. While some workers have reconstructed vertical or near-vertical neck postures, other have reconstructed straight, horizontal or even downward-sloping necks (Fig. 1).

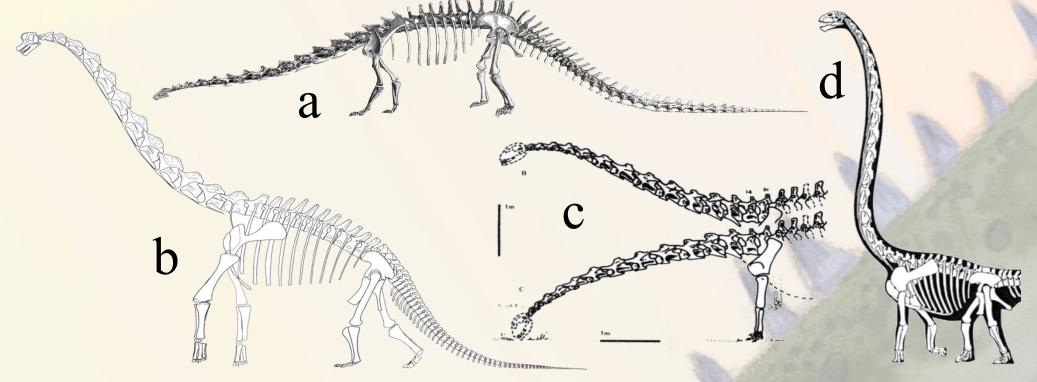


Fig 1. Views on sauropod neck posture have varied considerably through the years. (a) Diplodocus carnegii after Hatcher; (b) Giraffatitan brancai after Janensch; (c) range of vertical neck movement postulated for Cetiosaurus oxoniensis by Martin; (d) Omeisaurus after Paul.

A FASHIONABLE HYPOTHESIS IS THAT SAUROPODS HELD THEIR NECKS IN 'NEUTRAL POSE'

In order to determine sauropod neck posture in life, Stevens & Parrish (1999) used digital modelling of reconstructed zygapophyseal surfaces. One of their primary assumptions was that animals habitually maintain extensive zygapophyseal overlap throughout the cervical series. The pose with maximum overlap was termed the osteological neutral pose (ONP). Stevens & Parrish argued that ONP corresponds with the habitual pose adopted by an animal in life, claiming that "with no known exception, the curvature characteristic of the axial skeleton of a given vertebrate arises, not from chronic flexion out of the neutral position, but from the morphology of the vertebrae in their undeflected state" (Stevens & Parrish 2005a, p. 182).

By reconstructing sauropod necks in ONP, Stevens & Parrish (1999) argued that the necks of the diplodocids *Diplodocus* and *Apatosaurus* were habitually held at or below horizontal, and that they could not be raised far above horizontal (Fig. 2). They later argued that the same was true for *Cetiosaurus*, *Dicraeosaurus*, *Camarasaurus*, *Giraffatitan* and *Euhelopus*, and concluded that "all sauropods examined held their heads at or below the height of the shoulder in neutral posture" (Stevens & Parrish 2005b, p. 212). The hypothesis that ONP reflects life posture has mostly gone unchallenged, though Upchurch (2000) and Christian & Dzemski (2007) published objections. A lack of additional research, and the absorption of Stevens & Parrish's conclusions into museum displays, television series and the popular literature, has created the impression that horizontal-necked sauropods represent the current consensus view.

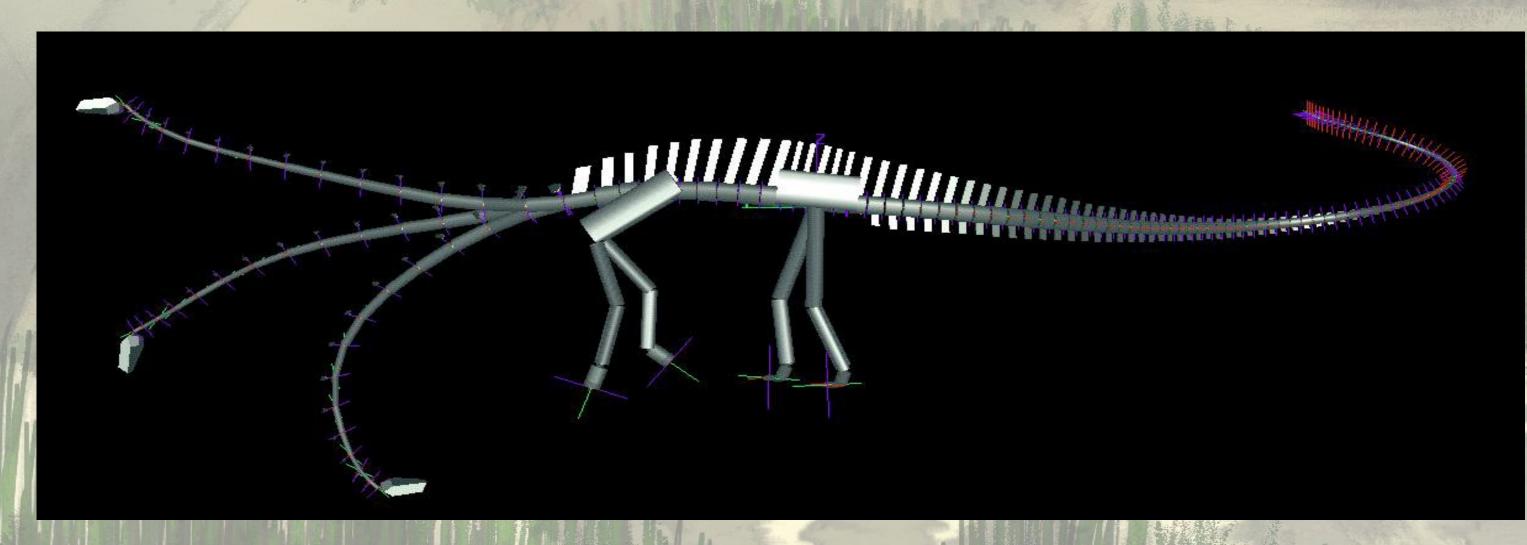


Fig. 2. Neutral pose for *Diplodocus*, along with the highest and lowest positions that, according to Stevens & Parrish (1999), the neck could achieve. From Stevens (2002: fig. 6a).

EXTANT TETRAPODS DO NOT HOLD THEIR NECKS AND HEADS IN 'NEUTRAL POSE'

We were interested in testing the assertion that living animals maintain their necks in ONP. A substantial literature on extant lissamphibians, mammals, squamates, turtles, crocodilians and birds incorporates X-ray data on the normal poses adopted in relaxed individuals (i.e., animals that are not foraging, feeding, or stressed). We reviewed this literature and also obtained unpublished X-rays. In extant mammals and birds, head and neck posture is consistent: (i) the cervical column is held nearly vertical during normal functioning; (ii) the middle part of the neck is habitually held relatively rigid; (iii) the neck is maximally extended at the cervico-dorsal junction and maximally flexed at the craniocervical junction; and (iv) it is the cranio-cervical and cervico-dorsal junctions that are primarily involved in raising and lowering the head and neck. These observations extend across animals that appear short-necked, such as rodents and lagomorphs among mammals (Vidal et al. 1986, Graf et al. 1992, 1995) (Figs 3b-d) and parrots among birds. Furthermore, elevated neck postures are not unique to birds and mammals: salamanders, lizards (Fig. 3e), crocodilians and turtles also maintain an extended cervico-dorsal junction and flexed cranio-cervical junction and keep the neck inclined above the horizontal (Vidal et al. 1986, Owerkowicz et al. 1999, Simons et al. 2000, Landberg et al. 2003).

Maintaining the neck in an elevated posture is not a concern in terms of metabolic cost, as "the resting position of the head-neck ensemble, including the upright posture of the cervical vertebral column, is almost exclusively the product of passive mechanical constraints [allowing] the maintenance of the resting head-neck posture with minimum energy expenditure" (Graf et al. 1992, p. 132).

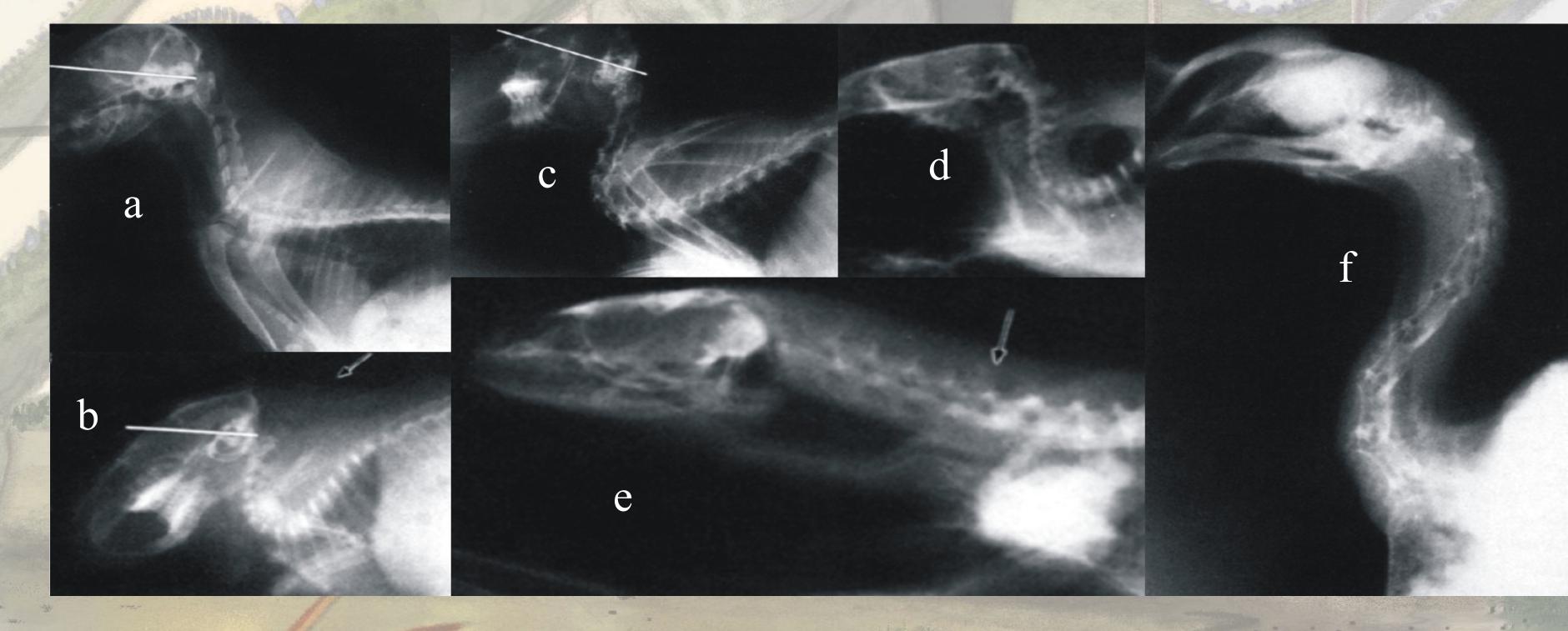


Fig. 3. X-rays reveal that extant tetrapods maintain their necks in elevated postures, with extended cervico-dorsal junctions and flexed cranio-cervical junctions. Strong neck elevation (where the middle part of the cervical series is held near-vertical) is present in mammals (a-d) and birds (f) as well as some turtles and crocodilians. More modest neck elevation (c. 20-40° relative to the dorsal series) is present in lissamphibians, squamates (e) and most crocodilians. (a) cat; (b) guinea-pig; (c) rabbit; (d) rat; (e) Savannah monitor; (f) chicken. Images from Vidal et al. (1986).

We sought to test ONP further by manipulating the vertebrae of modern mammals (lagomorphs) and birds (galliforms). Posing the vertebrae in ONP (i.e., with zygapophyses maximally overlapped) results in a ventrally deflected or only slightly raised neck pose very different from that maintained in life (Taylor et al. 2009). In order to reconstruct the neck postures determined by X-ray observations, the cervical series has to be substantially more elevated than ONP: indeed, life posture is so elevated that this pose cannot be easily achieved by the manipulation of dry bones alone. It is apparent that the soft-tissue of the neck (e.g., intervertebral cartilage) enables greater flexibility in the neck than the bones alone suggest.

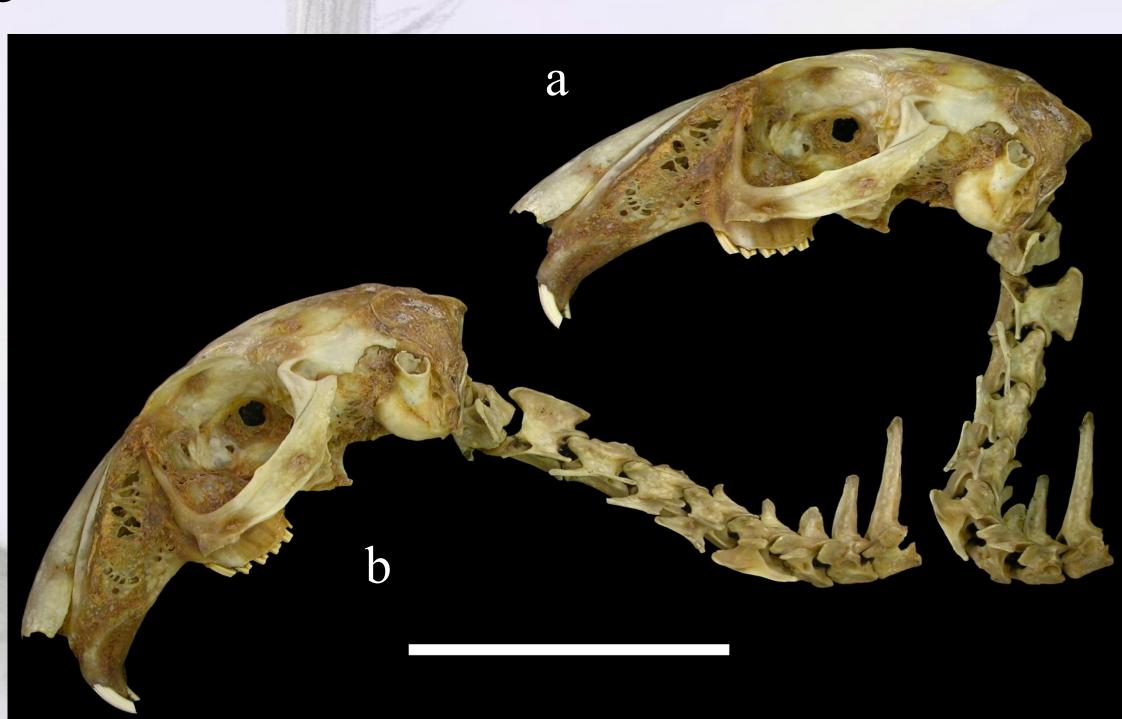


Fig. 4. Cape hare *Lepus capensis* RAM R2, illustrating (a) pose most compliant with that seen in X-rays and (b) ONP: skull, cervical vertebrae 1-7 and dorsal vertebrae 1-2. Note the very weak dorsal deflection of the base of the neck in ONP, contrasting with the much stronger deflection illustrated in a live rabbit by Vidal et al. (1986: fig. 4). Scale bar 5 cm.

The proposal that ONP represents the normal posture adopted during life is falsified.

AN ELEVATED NECK POSTURE IS THE NULL HYPOTHESIS FOR ALL EXTINCT TETRAPODS, INCLUDING SAUROPODS

Elevated neck posture is widespread throughout crown-Tetrapoda. Phylogenetic bracketing shows that an elevated neck is found in all extant outgroups to Sauropoda, including Aves, Crocodylia, Squamata, Testudines and Mammalia (Fig. 5). In the evidence of absence to the contrary, an elevated neck posture should be assumed for sauropods, despite their 'extreme' morphology. There is no indication that sauropods were anomalous: speculation that they evolved novel mechanisms of neck support distinct from those of extant tetrapods (such as the ventral neck bracing a pneumatostatic system) lacks evidence. It is most parsimonious to assume that the necks of sauropods were supported by the same mechanisms as in their extant outgroups, and in similar postures.

The realisation that elevated necks are widespread throughout Tetrapoda is not relevant only to sauropods. Reconstructions which provide other fossil tetrapods with flexed cervico-dorsal junctions and extended cranio-cervical junctions should be regarded as flawed and at odds with the evidence from living animals.

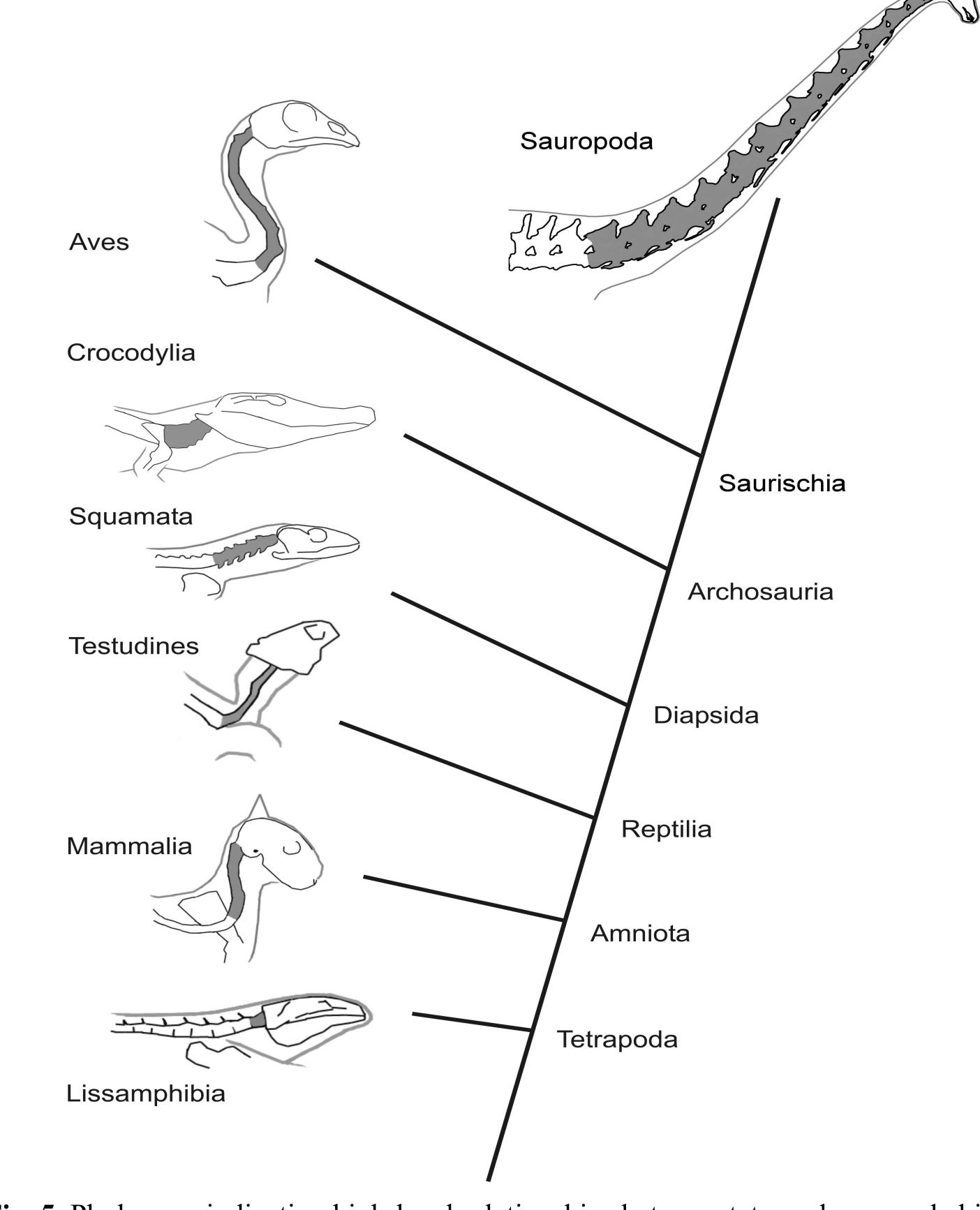


Fig. 5. Phylogeny indicating high-level relationships between tetrapod groups, habitual neck posture in extant groups, and inferred posture in sauropods. Cervical vertebrae shaded. Lissamphibia: *Ambystoma tigrinum*, after Simons et al. (2000: fig. 4); Mammalia: *Felis catus*, after Vidal et al. (1986: fig. 3B); Testudines: *Terrapene carolina*, after Landberg et al. (2003, fig. 8); Squamata: *Varanus exanthematicus*, after Owerkowicz et al. (1999: fig. 2A); Crocodylia: *Alligator mississippiensis*, after unpublished photo; Aves: *Gallus gallus*, after Vidal et al. (1986: fig. 7); Sauropoda: *Diplodocus carnegii*, modelled after vertebrae in Hatcher (1901: fig. 4, pl. 3).

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