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HEMIVERTEBRAE AS PATHOLOGY AND AS A WINDOW TO BEHAVIOR IN THE FOSSIL RECORD

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ABSTRACT

An extinct feline ecomorph *Hoplophoneus* was afflicted with a congenital anomaly (hemivertebra) not previously observed in cats and not previously reported in fossil mammals. The position of the hemivertebrae provided little opportunity for other cervical vertebrae to compensate for the resultant 40-degree deformity.

Introduction

Hemivertebrae are the result of congenital defects in vertebral segmentation. Vertebrae develop in a segmentally-coordinated manner from multiple ossification centers (Riedel-Kruse *et al.*, 2007). When an ossification center fails to develop or fuse, hemivertebrae result. Hypoxia, genetic effects and toxins disrupt fusions (Balie *et al.*, 1986; Erol, Kusumi, *et al.*, 2002; Erol, Trach, *et al.*, 2004), as well as a hemimetameric segmental shift (Shawen *et al.*, 2002; Tian *et al.*, 2006).

There are four varieties of hemivertebrae, listed in order from most to least frequent in humans (McMaster, 2001): Fully segmented, semi-segmented, non-segmented and incarcerated. A fully segmented hemivertebra is completely separated from adjacent vertebrae by normal disk spaces. Scoliosis develops at a rate of 1 to 2 degrees per year in humans. A semi-segmented hemivertebra, synostosed to an adjacent vertebra, is bordered by only one disk space, resulting in scoliosis of up to 40 degrees in humans. Non-segmented hemivertebrae (not separated from adjacent vertebrae by disk spaces) have no growth potential and do not cause significant scoliosis. Incarcerated hemivertebrae fit an area "scalloped out of the adjacent vertebrae" (Watson *et al.*, 1988) and are associated with scoliosis of less than 20 degrees in humans. A hemivertebra must be distinguished from the wedge vertebrae, which reflects partial failure of the vertebra to form on one side, although it retains two pedicles (Bailey and Morgan, 1992).

Hemivertebrae have been observed at a frequency of 5 to 10 per 10,000 births in humans (Wynne-Davies, 1975) and have been reported in contemporary horses, cattle, scimitar-horned Oryx, dogs, rabbits, chimpanzees, mandrills and snakes (Agerholm *et al.*, 2001; Baur, 1891; Ettinger & Feldman, 2005; Harwell, 1982; Morgan, 1968; Nagahata *et al.*, 2002; Schultz, 1915). Reports in the fossil record include an early Triassic brachyopid stereospondylis *Bothriceps australis* (Warren *et al.*, 2011), a Middle Triassic temnospondyl amphibian (Witzmann, 2007), an Upper Jurassic plesiosaur *Cimoliasaurus plicatus* (Lydekker, 1889), an ornithischian dinosaur *Dysalotosaurus lettowvorbecki* (Janensch, 1934; Witzman *et al.*, 2008) and a Cretaceous *Hypacrosaurus* (Rothschild & Tanke, 2006). Hemivertebrae, sometimes referred to as wedge-shaped vertebrae, are the "most clinically significant vertebral anomaly in the dog" (Colter, 1993), especially screw-tailed breeds such as Boston terrier, pug, and English and French bulldogs.

While vertebral anomalies are common in domestic cats (Newitt *et al.*, 2008), hemivertebrae have not been reported. Vertebral malformations, in general, seem rare in non-domestic feline ecomorphs. The term ecomorphs is used to define a category of animals with a feline habitus (Naples, Martin & Babiarz, 2011), independent of phylogeny (*e.g.*, Nimravidae, Felidae). One of the few reports of a feline is that of Galloway *et al.,* (2002) of atlantal vertebral malformations in lions. We report the first notation of a hemivertebra in a feline ecomorph.

Materials and Methods

An incomplete nimravid skeleton, BIOPSI (Babiarz Institute of Paleontological Studies) 0235, lacking the skull, was collected from the Oligocene (33.7 to 23.8 million years ago) Brule Formation of Sheridan County, South Dakota. Only postcranial remains were discovered. The vertebral column was represented by cervical vertebrae (C-2 through C-6 and fragments of C-7), thoracic vertebrae (T-1, T-7, T-11, T-13), lumbar vertebrae, and distal caudal vertebral fragments. Preserved forelimbs included left humerus, radius, ulna, metacarpals and bony elements of the paw and proximal portions of the right ulna and radius. Right patella, tibia, fibula and a nearly complete right pes, and left calcaneum, left navicular, and left distal pedal elements. Vertebrae and tibiae from known *Hoplophoneus primaevus* specimens [BHI (Black Hills Institute) 6431; BIOPSI 0245, BIOPSI 0246] and tibiae from known *Dinictis felina* specimens (BIOPSI 0140, BIOPSI 0146) were examined macroscopically. X-rays were made of the vertebrae, using digital film/screen combination at exposures (40 Kvp, 22 MaS), a technique typically applied to human knees. Standard deviation and confidence intervals were calculated for tibial length (tibial plateau to the tip of lateral malleolus) in *Hoplophoneus primaevus* and *Dinictis felina.* Comparison was made with vertebrae of known *Hoplophoneus primaevus* (BHI 6431; BIOPSI 0245, BIOPSI 0246). Casts of the hemivertebrae were reposited in the University of Kansas Vertebrate Paleonotlogy collection (KUVP-C-2711).

Results

We recognized the incomplete skeleton BIOPSI 0235 as belonging to a nimravid, on the basis of tibial characteristics (Naples *et al.*, 2011). The only other recognized nimravids from this site are the gracile, long-legged *Dinictis felina* and the robust, short-legged *Hoplophoneus primaevus*. Epiphyseal fusion confirms that our specimen is an adult. The length of the tibia in BIOPSI 0235 is 139 mm, well within the 95% confidence intervals for *Hoplophoneus primaevus* (119.0-214.4 mm) and significantly less than that for *Dinctis felina* (149.6-227.9 mm). Examination of known *Hoplophoneus primaevus* reveals that cervical vertebra 3 normally has a posteriorly situated spinous process. This feature can be surmised from the broken edges where the spine was situated in this specimen although most of the spinous process is missing. There is an embayment (sulcus) along the dorsal surface of the centrum for the neural canal. The anterior edge of the centrum is inclined with the dorsal edge projecting anteriorly. Both prezygopophyses are broken off and missing. The left transverse process is preserved and its base projects anteriorly, causing a slight overlap of the centrum itself. Apparently the same condition exists for the right transverse process, although it is missing the right transverse process. The transverse process is oriented posteriorly and slightly tapers along its length. The distal termination of the transverse process is incomplete, apparently due to postmortem damage. Only the right postzygapopohysis is preserved.

The malformed hemivertebral segment of BIOPSI 0235 is positioned between cervical vertebrae 3 and 4 (figure 1). The hemivertebra is 10 mm long and fused to the left side of the posterior aspect of centrum 3. It has an articulating surface that fits into a facet on the left anterior face of centrum 4. The hemivertebra is only half as wide as either centra 3 or 4. It acts as a wedge, forcing malalignment of cervical vertebra 4 by 40 degrees. This anomaly is evidenced by the ventral groove running from the left anterior edge of the centrum across to the right posterior edge. The right transverse process (although it is broken off and missing) and the right postzygopophysis actually reside on the hemivertebra. The left transverse process is nearly complete and in its normal position on cervical 3. Because the remainder of the neural arch is broken off and missing, prezygapophyses and the spinous process are not present. Interestingly, the shape of the neural canal is distorted (compressed dorsoventrally) on both cervicals 3 and 4 (the fossil does not show any sign of postmortem deformation).

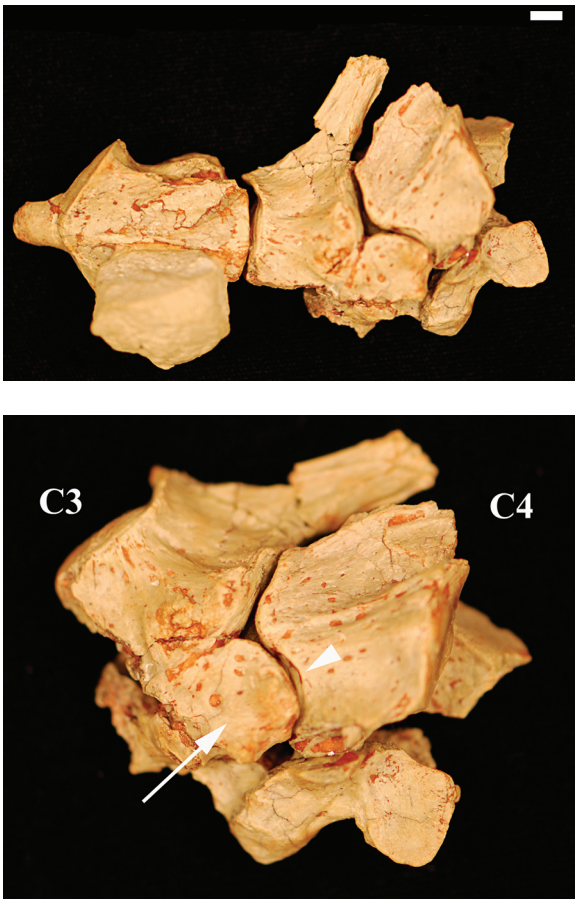

Figure 1. Ventral view of articulated cervical vertebrae 2, 3, & 4. A) Vertebral series. Scale bar equals 5 mm; B) Close up of afflicted vertebrae: Hemivertebra at C3 (arrow) and defect in C4 (arrowhead). Scale bar is 1 cm. Photography by D. Burnham.

As mentioned above, the next cervical in the series is also affected by the hemivertebra. The articulation that accommodates the hemivertebra is inclined dorsoventrally so that it encroaches on the left lateral side of the centrum. The prezygopophyses are set at different angles. It is unknown whether this is postmortem damage or a change that occurred to accommodate a twisted neck. The postzygapophyses are normal. The spinous process and the transverse processes are missing.

Discussion

Hoplophoneus primaevus is an extinct cat-like animal, about the size of a small jaguar, from the family Nimravidae that ranged in North America during the Late Eocene (Chadronian) to the mid Oligocene (Upper Whitneyan) from 38 to 33.3 million years ago (Bryant, 1991; Martin, 1998). Their outward appearance is similar to modern felines, but they lack the septally-divided auditory bulla found in true cats (Hunt, 1987). These saber tooth ecomorphs have a mandibular flange. The only recognized nimravids from this site are the gracile, long-legged *Dinictis* and robust, short-legged *Hoplophoneus*, similar to that of *Megantereon*, considered the ancestor of *Smilodon*.

This paper is the first report of hemivertebra and scoliosis in a feline ecomorph, in contrast to its common recognition in canids (Colter, 1993). The hemivertebra reported here is of the semi-segmented variety and produced the anticipated 40-degree neck angulation. This differs from an incarcerated hemivertebra, which does not produce angulation/scoliosis. Similar hemivertebra-induced scoliosis has been previously observed in the fossil record in a Middle Triassic temnospondyl amphibian (Witzman, 2007). Hemivertebrae sometimes occur as a complication of medical intervention. Treatment of struvite urolithiasis (stones) with the urease inhibitor acetohydroxamic acid has resulted in congenital hemivertebrae in beagles (Bailie *et al.*, 1986).

Hemivertebrae have been reported in the fossil record, but this appears to be the first that included posterior cervical elements (Warren *et al.*, 2011; Witzmann, 2007; Lydekker, 1889; Janensch, 1934; Witzman *et al.*, 2008; Rothschild & Tanke, 2006). Preservation of vertebral elements is rarely discussed in commentaries on hemivertebrae (McMaster, 2001; Bailey & Morgan, 1992; Ruberte *et al.*, 1995), except for preservation of the neural arch when atlas (C-1) is affected (Watson *et al.*, 1988). The only comment on posterior elements in the human surgical literature was the incidental notation that a pedicle present on a hemivertebra also was excised with the hemivertebra (Bollini *et al.*, 2006).

Hemivertebrae of the cervical spine are rare (Besalti *et al.*, 2005; Ruf *et al.*, 2005). The animal in this report suffered the same type of cervical hemivertebra as Besalti *et al.* (2005) reported in a dog. The position of the cervical hemivertebrae provides little opportunity for other cervical vertebrae to compensate for the deformity (Ruf *et al.*, 2005), thus resulting in significant neck tilt. It is unknown what neurologic disorders may have been associated with the compression of the neural canal.

Hemivertebrae are commonly associated with other congenital anomalies (Basu *et al.*, 2002) as noted in this specimen's cervical vertebra 4. The macroscopic appearance of the abnormality in the vertebra (cervical vertebra 4) adjacent to the hemivertebra in *Hoplophoneus primaevus* mirrors that observed in a 35 year old 16th century human with the same congenital condition (Aceves-Avila *et al.*, 1998). This observation illustrates the spectrum of congenital vertebral abnormalities found in the fossil record and provides speculation that an off balance view of the world is still compatible with survival.

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