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J. T. and K. T. conducted taxonomical aspects of this study. T. M. conducted the CT scan of the studied specimen and interpreted the results with K. T. All authors wrote this manuscript.

Description of a titanosauriform (Sauropoda, Dinosauria) cervical vertebra from the Lower Cretaceous Kanmon Group, southwestern Japan

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Abstract

A fragmentary and yet to date the largest single bone element from the Lower Cretaceous Kanmon Group in Kyushu Island, southwestern Japan is described. This specimen has a fossa and lenticular foramen on its lateral surface and internal chambers of both large and small sizes. It was identified as the cervical vertebra of a titanosauriform sauropod dinosaur mainly based on such pneumatic structure. This specimen represents the first titanosauriform to be described from the Kanmon Group.

Keywords: Cretaceous, Kanmon Group, Titanosauriformes, vertebral pneumaticity, Wakino Subgroup

Introduction

The Lower Cretaceous Wakino Subgroup, which forms the lower part of the Kanmon Group, is exposed in western Honshu and northern Kyushu islands, southwestern Japan (Fig. 1; Ota *et al.*, 1979; Nakae *et al.*, 1998). This subgroup has long been studied stratigraphically and paleontologically (Matsumoto, 1951; Hase, 1960; Ota, 1960; Ota *et al.*, 1979; Uyeno, 1979; Yabumoto, 1994). Fossils of mollusks, algae, freshwater fishes, turtles, crocodilians and dinosaurs were reported from the Wakino Subgroup (Ishijima, 1979; Ota *et al.*, 1979; Okazaki, 1992, 1994; Tanoue and Okazaki, 2014; Sonoda *et al.*, 2015).

Although the Wakino Subgroup yields many fragmentary specimens considered to be dinosaurs, they have not been studied thoroughly due to poor preservation and the extremely hard matrices they are embedded in. Only two specimens have been described to date. The first specimen is a theropod (Okazaki, 1992) and the second is a neoceratopsian (Tanoue and Okazaki, 2014), both of which are tooth specimens. Recent preparation and observation of fragmentary fossil bones imply the dinosaurian diversity of the subgroup to be higher than was our previous understanding. The largest fossil bone specimen from the Wakino Subgroup is described in this paper.

Anatomical abbreviations.—**cml**, camella; **cmr**, camera; **pcdl**, posterior centrodiapophyseal lamina; **pf**, pneumatic foramen; **pocdf**, postzygapophyseal centrodiapophyseal fossa

Institutional abbreviations.—**AMNH**, American Museum of Natural History, New York City, U.S.A.; **FRDC**, Fossil Research and Development Center of the Third Geology and Mineral Resources Exploration Academy of Gansu Province, Lanzhou, P. R. China; **KMNH**, Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan; **PMU**, Palaeontological Museum, Museum of Evolution, Uppsala, Sweden

Geological setting

The Lower Cretaceous Kanmon Group is exposed in Yamaguchi (western end of Honshu Island) and Fukuoka (northern Kyushu Island) prefectures, southwestern Japan (Figure 1A; Matsumoto, 1951; Hase, 1960; Ota, 1960; Ota *et al.*, 1979; Nakae *et al.*, 1998). It was formed in an intra-arc basin along the eastern margin of Asia (Aoki *et al.*, 2014; Nakahata *et al.*, 2016). The Kanmon Group includes the Wakino and Shimonoseki subgroups in ascending order (Matsumoto, 1951). The Wakino Subgroup consists of non-marine deposits and is 1,000 to 1,200 meters thick (Ota *et al.*, 1979). The Wakino Subgroup is characterized by non-marine beds which consist of conglomerate, sandstone, reddish purple-sandstone and acidic tuff (Seo *et al.*, 1992; Nakae *et al.*, 1998). In the Kokura area, Kitakyushu City, Nakae *et al.* (1998) divided the subgroup into Dobaru, Takatsuo, Gamo and Kumagai formations in ascending order (Figure 1B). The Shimonoseki Subgroup is composed of andesite, pyroclastic deposits and non-marine beds (Uyeda, 1957; Nakae *et al.*, 1998). The U-Pb ages of zircon in rhyolitic tuffs of the Wakino and Shimonoseki subgroups indicate they are both Albian (Miyazaki *et al.*, 2019).

The Wakino Subgroup in Fukuoka Prefecture has been known for numerous well-preserved freshwater fishes since the 1950s (e.g. Ota, 1955; Uyeno, 1979; Yabumoto, 1994; Okazaki, 2016). In marked contrast, only a few fragmentary materials of terrestrial vertebrates including turtles (Sonoda *et al.*, 2015), crocodiles (Okazaki, 1994) and dinosaurs (Okazaki, 1992; Tanoue and Okazaki, 2014) have been reported from the Wakino Subgroup. Dinosaurian eggshell is the only vertebrate specimen recovered from the Shimonoseki Subgroup to date (Imai *et al.*, 2020).

The studied specimen was collected by Yoshihiko Okazaki in 1996 from the middle Gamo Formation in the Kokura area, whose outcrop is in a quarry (Figure 1A, B). The Gamo Formation is composed of conglomerate, sandstone and mudstone layers yielding freshwater gastropods and osteichthyes (Ota *et al.*, 1979; Yabumoto, 1994; Nakae *et al.*, 1998). The studied specimen was recovered from a siltstone layer considered to be a lacustrine deposit. Siltstone containing the studied specimen was severed and the anteroventral portion of the specimen was removed for commercial purpose prior to collection. Although fragmentary, it is the largest element of a vertebrate recovered from the Wakino Subgroup to date.

Material and Methods

The studied specimen (KMNH VP 600014) is a partial cervical vertebra housed at the Kitakyushu Museum of Natural History and Human History (Figure 2). It was embedded in massive siltstone.

The specimen has initially been prepared with chisels, hammers and an air pen (Desoutter VP2-X). Preparation was halted to prevent further damage when the lateral surface was exposed. For description of its internal structure, computed tomography (CT) images were obtained with a Toshiba Toscanner 23200 mini at the X-Earth Center, Kumamoto University in addition to observation of artificially produced sections (Figure 3). The studied specimen was scanned at 300 kV, 2 mA and 2048 × 2048 pixel matrix. Scanned data were converted to PNG files by ImageJ (Schneider *et al.*, 2012).

Britt (1993, 1997) proposed the terms camera (large chamber) and camella (small chamber) to describe internal chambers of pneumatic bones, both of which were further refined by Wedel *et al.* (2000a). Following the definitions of Wedel *et al.* (2000a), internal chambers of the studied specimen were classified into camerae and camellae as shown in Figures 2 and 3. A chamber was identified as a camera if its minimum length exceeds 20 mm and maximum thickness of its septa are equal to or wider than 2 mm in this study. Any relatively small chamber was specified as a camella if its minimum length is shorter than 20 mm and maximum thickness of its septal walls are equal to or narrower than 2 mm. The geometry of the chambers and branching patterns proposed in Wedel *et al.* (2000a) to distinguish a camera (round cavity and regular branches) from a camella (angular cavity and irregular branches, respectively) were not considered in this study due to the distorted nature of the studied specimen. The nomenclature of vertebral laminae and fossae follows Wilson (1999) and Wilson *et al.* (2011), respectively. Classification of vertebrae based on pneumatic characters proposed by Britt (1993, 1997) and Wedel *et al.* (2000a) is employed here.

Systematic paleontology

Order Saurischia Seeley, 1887

Suborder Sauropoda Marsh, 1878

Neosauropoda Bonaparte, 1986

Titanosauriformes Salgado, Coria and Calvo, 1997

Titanosauriformes indet.

Figure 2

Description.—KMNH VP 600014 is an incomplete fragmentary bone fossil (Figure 2). The external surface is preserved only on the left lateral side. An artificially produced anteroventral section exposes the internal structure of the specimen (Figure 2C, D). In lateral view a distinctive lenticular foramen lies in the central region of the preserved specimen, with the proximal portion of a laminar structure immediately dorsal to it (Figure 2A, B). Other regions exposing the matrix within this specimen cannot be identified as foramina because they may have been formed by postmortem perforation or breakage. The long axis of the lenticular foramen is used for reference to measure the studied specimen because anteroposterior and dorsoventral directions cannot be ascertained accurately. The length and height of the specimen parallel to and perpendicular to the major axis of the foramen are 380 mm and 165 mm, respectively as preserved (Figure 2A). The length along the major axis of this foramen is 66 mm and that along the minor axis is 20 mm. The maximum mediolateral width of the specimen is 59 mm as preserved.

The lenticular foramen is connected medially to an internal chamber (Figures 2E, F, 3E). Other chambers can be recognized in Figures 2C, D and 3C, E, F. These chambers indicate pneumatic internal structure of the specimen. Among the Cretaceous vertebrates, cervical vertebrae, ribs, scapulae, scapulocoracoids and ilia can be elongate, pneumatic and longer than KMNH VP 600014 (e.g. Janensch, 1950; Wedel *et al.*, 2000b; Sereno *et al.*, 2008; Cerda *et al.*, 2012). The pneumatic foramen in a rib is located on the capitulum, tubercle or in the proximal region of the shaft (Marsh, 1896; Gilmore, 1936; Lovelace *et al.*, 2007; Cerda *et al.*, 2012). Although the pneumatic foramina in ribs can be associated with ridges extending from the capitulum and tubercle to the shaft, the studied specimen lacks a bifurcated configuration (e.g. Marsh, 1896; Gilmore, 1936). The pneumatic foramen in the scapula or scapulocoracoid is not lenticular and is much smaller than that of KMNH VP 600014 (Cerda *et al.*, 2012). Although some pneumatic foramina in ilia are lenticular, laminar structure is absent. Only cervical vertebra can be associated with both lenticular pneumatic structure including fossae and foramina, and laminar structure among these elements (e.g. Hatcher, 1901; Gilmore, 1936). Therefore, KMNH VP 600014 could be identified as a cervical vertebra.

Azhdarchid pterosaurs and sauropods both have elongate pneumatic vertebra in their cervical region, some of which exceed the length of KMNH VP 600014 (e.g. Hatcher, 1901; Lawson, 1975; Frey and Martill, 1996; Wedel *et al.*, 2000b). Elongate cervical vertebrae of azhdarchids are dorsoventrally low even when their neural spines are included (Witton, 2013). The studied specimen, if complete, would have been higher even considering the postmortem distortion. Although azhdarchid vertebral column is pneumatized (Claessens *et al.*, 2009), its cervical centra lack evident pneumatic foramina on the lateral surface unlike the studied specimen (Pereda-Suberbiola *et al.*, 2003; Witton, 2013). These characters preclude assigning KMNH VP 600014 to azhdarchids. Sauropods have a posterior centrodiapophyseal lamina system on the anterior and mid-cervical vertebrae, which is partially preserved in the studied specimen dorsal to the lenticular foramen as noted (Upchurch *et al.*, 2004). KMNH VP 600014 thus can be referable to sauropods.

A shallow fossa encloses the lenticular pneumatic foramen at which the intraosseous diverticulum of an air sac entered the centrum (Figure 2A, B, E, F; Wedel, 2003; O'Connor and Claessens, 2005). The depth of this fossa, however, may be due to compression during fossilization. Although only one lateral fossa is recognizable in KMNH VP 600014 with no other fossae bounded by laminae in between, other fossae may have excavated missing portions of the vertebra. Dorsal to the lenticular foramen is what may have been the proximal portion of posterior centrodiapophyseal lamina (pcdl), which is subsided medially possibly due to postmortem compression (Figure 2A, B). The preserved pcdl is 151 mm in length. A postzygapophyseal centrodiapophyseal fossa (pocdf) extends dorsally from the pcdl with a height of 36 mm at most (Figure 2A, B).

The neural spine, condyle, cotyle, prezygapophyses, postzygapophyses, diapophyses and parapophyses are not preserved.

Internal structure of the left side is relatively well-preserved. Although highly distorted, internal chambers can still be identified in cross sections and CT images (Figures 2C, D, 3C, E, F). They are not completely closed by osteal margins; the septal walls between chambers are perforated, though the perforations may have been formed by postmortem distortion. In observed cross sections, compact bone of the outer surface is the thickest, reaching 11 mm. The walls of internal septa are thinner with a thickness of 6 to 7 mm at most. The camera immediately ventral to the pneumatic foramen is the largest among recognizable chambers (Figures 2E, F, 3F). Although chambers are not preserved in the posterior region of KMNH VP 600014, camerae tend to be distributed in the central region, whereas camellae are in the anterior region (Figures 2C, D, 3C, E, F).

Classification and evolution of sauropod vertebrae based on pneumatic characters is summarized in Figure 4. Within Sauropoda, vertebrae of basally branching sauropod *Vulcanodon* and early eusarupods such as *Barapasaurus* and *Shunosaurus* are acamerate. Acamerate vertebrae have fossae but lack camerae or camellae (Jain *et al.*, 1979; Cooper, 1984; Britt, 1997; Wilson and Sereno, 1998; Wedel *et al.*, 2000a; Wedel, 2003). The procamerate vertebrae of *Haplocanthosaurus* also lack camerae or camellae (Wedel *et al.*, 2000a). The basally branching macronarian *Camarasaurus* has camerate vertebrae whose internal structure comprise camerae with cameral generations usually limited to three (Wedel *et al.*, 2000a; Wedel, 2003). Vertebrae of diplodocid *Diplodocus* and *Apatosaurus* are polycamerate. Polycamerate vertebrae also are composed of camerae internally but usually have three or more cameral generations and more branches at each generation than in camerate vertebrae (Wedel *et al.*, 2000a; Wedel, 2003). The internal structure of semicamellate vertebrae, which are recognized only in titanosauriforms such as *Brachiosaurus* and *Giraffatitan*, is composed of both camerae and camellae (Wedel *et al.*, 2000a; Schwarz and Fritsch, 2006; Taylor, 2009). *Mamenchisaurus* and early somphospondylians have camellate vertebrae that are entirely filled with numerous camellae (Young and Zhao, 1972; Russell and Zheng, 1993; Wedel *et al.*, 2000a; Wedel, 2003). With the exception of *Gondwanatitan*, whose partial cervical vertebra shows a camerate condition (Kellner and de Azevedo, 1999; Wedel, 2003), vertebrae of titanosaurians are somphospondylous which also comprise camellae internally (Wedel *et al.*, 2000a; Wedel, 2003). Although taxonomic classification based on juvenile specimens should be avoided, considering the size of the fragment KMNH VP 600014 is not likely to be the vertebra of a juvenile individual.

The presence of both camerae and camellae demonstrates the studied specimen is a semicamellate vertebra. KMNH VP 600014 therefore could have belonged to Titanosauriformes (Wedel *et al.*, 2000a; D'Emic, 2012).

Discussion

Although it is difficult to compare the centrum length of KMNH VP 600014 with other titanosauriform cervical vertebrae from the Lower Cretaceous of East Asia, the fragment from the Wakino Subgroup is longer than the third cervical of *Mongolosaurus haplodon* (263 mm; AMNH 6710), the only postaxial cervical vertebra of this specimen that has been recovered (Gilmore, 1933). It is also longer than the 11th cervical of *Euhelopus zdanskyi* (283 mm; PMU 24705/11), which is the longest vertebra without anterior convexity in its cervical series (Wiman, 1929; Wilson and Upchurch, 2009; Poropat and Kear, 2013). Even if the studied specimen was complete it would be possibly shorter than the seventh-to-last cervical of *Daxiatitan binglingi* (91 cm; FRDC: GSLTZP03-001), the longest among the ten posterior cervical vertebrae recovered (You *et al.*, 2008). Assuming that the preserved portion accounts for most of the centrum length, KMNH VP 600014 may have been a titanosauriform cervical vertebra of intermediate length relative to cervical vertebrae of other titanosauriforms in the Early Cretaceous of East Asia.

KMNH VP 600014 is the largest single bone fossil from the Kanmon Group to date. It is also of the largest animal known from the group. This specimen represents the first titanosauriform from the group to be described. In addition to the fossil teeth of a theropod and a neoceratopsian, and the oospecies *Multifissoolithus shimonosekiensis*, the occurrence of this specimen demonstrates the diversity of dinosaurs from the Kanmon Group to be higher than previously thought (Okazaki, 1992; Tanoue and Okazaki, 2014; Imai *et al.*, 2020). It is evident that titanosauriforms could feed on higher vegetation than neoceratopsians, and that these two herbivores were able to coexist with little or no feeding competition.

Early Cretaceous titanosauriforms have been recovered from various areas in East Asia including Russia (Averianov *et al.*, 2002), Mongolia (Gilmore, 1933; Ksepka and Norell, 2006), China (Wang *et al.*, 2007; You *et al.*, 2008; Lü *et al.*, 2013), South Korea (Lim *et al.*, 2001; Park, 2016), Laos (Allain *et al.*, 1999) and Thailand (Martin *et al.*, 1994). Table 1 shows a list of titanosauriform specimens from the Cretaceous of Japan. KMNH VP 600014 adds to the abundance of titanosauriforms in East Asia. It is among the youngest from the Lower Cretaceous in Japan, along with *Tambatitanis* *amicitiae* from the Sasayama Group (Saegusa and Ikeda, 2014). Two partial neural arches of *Fukuititan nipponensis* from the Tetori Group and the atlas and fragmentary cervical vertebra of *T. amicitiae* are the only cervical specimens of titanosauriforms from Japan to date (Azuma and Shibata, 2010; Saegusa and Ikeda, 2014). Due to little or no overlap of preserved portions, comparison of these cervical specimens with KMNH VP 600014 is impracticable. Instead, the studied specimen provides new information about the anatomy of titanosauriform cervical vertebrae from the Cretaceous of Japan.

Conclusions

The largest single bone element from the Kanmon Group to date was identified as the cervical vertebra of a titanosauriform sauropod dinosaur based on its pneumatic structure. The discovery of the first titanosauriform specimen from the group offers important insight into its terrestrial vertebrate fauna. KMNH VP 600014 may also add to the diversity of titanosauriforms in the eastern margin of East Asia in the Early Cretaceous. Although mostly fragmentary, recovery of other materials from the Wakino Subgroup should provide more information on the diversity of the Early Cretaceous dinosaur fauna in East Asia.

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Figure and table captions

Figure 1. Distribution of the Kanmon Group in northern Kyushu Island, Japan and composite columnar section of the Wakino Subgroup. **A**, Distribution of the Wakino and Shimonoseki subgroups of the Kanmon Group. Arrow indicates the locality where the studied specimen was collected. **B**, composite columnar section of the Wakino Subgroup in Kokura area. Abbreviation: Fm, Formation. Modified after Nakae *et al.* (1998).

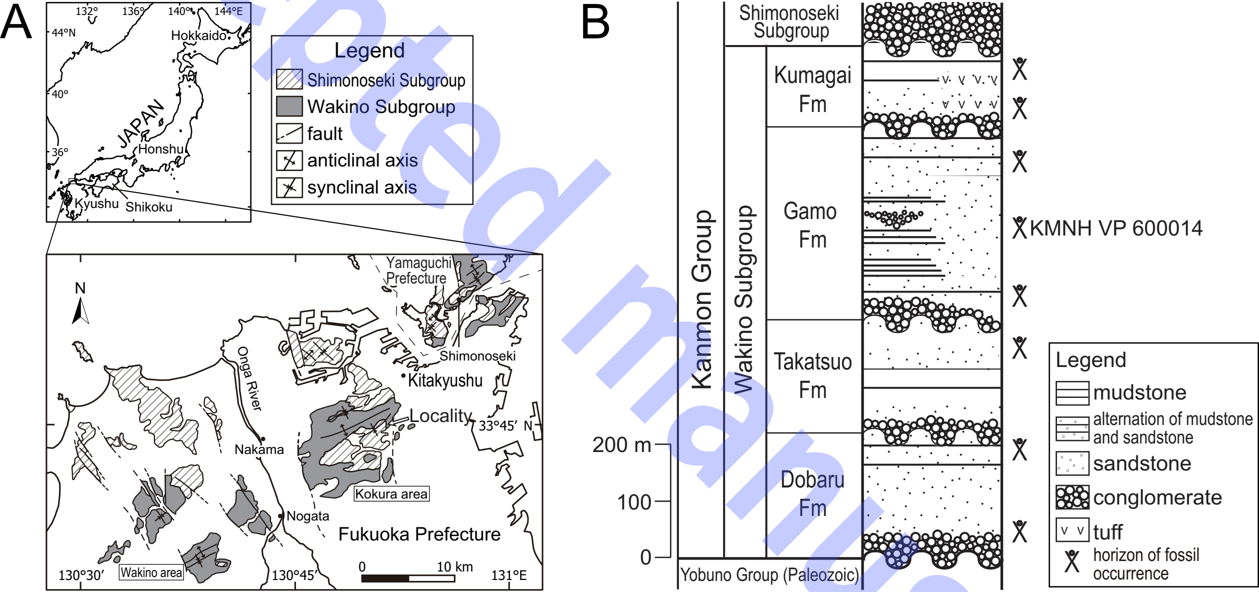
Figure 2. Photographs and interpretative illustrations of KMNH VP 600014. **A**, left lateral view; **B**, interpretative illustrations of A with hypothetical outline of the vertebra in dashed lines; **C**, ventral view; **D**, interpretative illustrations of C with outline of the matrix in dotted line; **E**, anteroventral view of the broken surface (the thickest line in B); **F**, interpretative illustration of E with outline of the matrix in dotted lines and the largest camera in this specimen labeled “cmr*”. Anterior: to the left in A–D; dorsal: to the top in A, B, E, F; lateral: to the top in C, D and to the right in E, F. Scale bars: 5 cm.

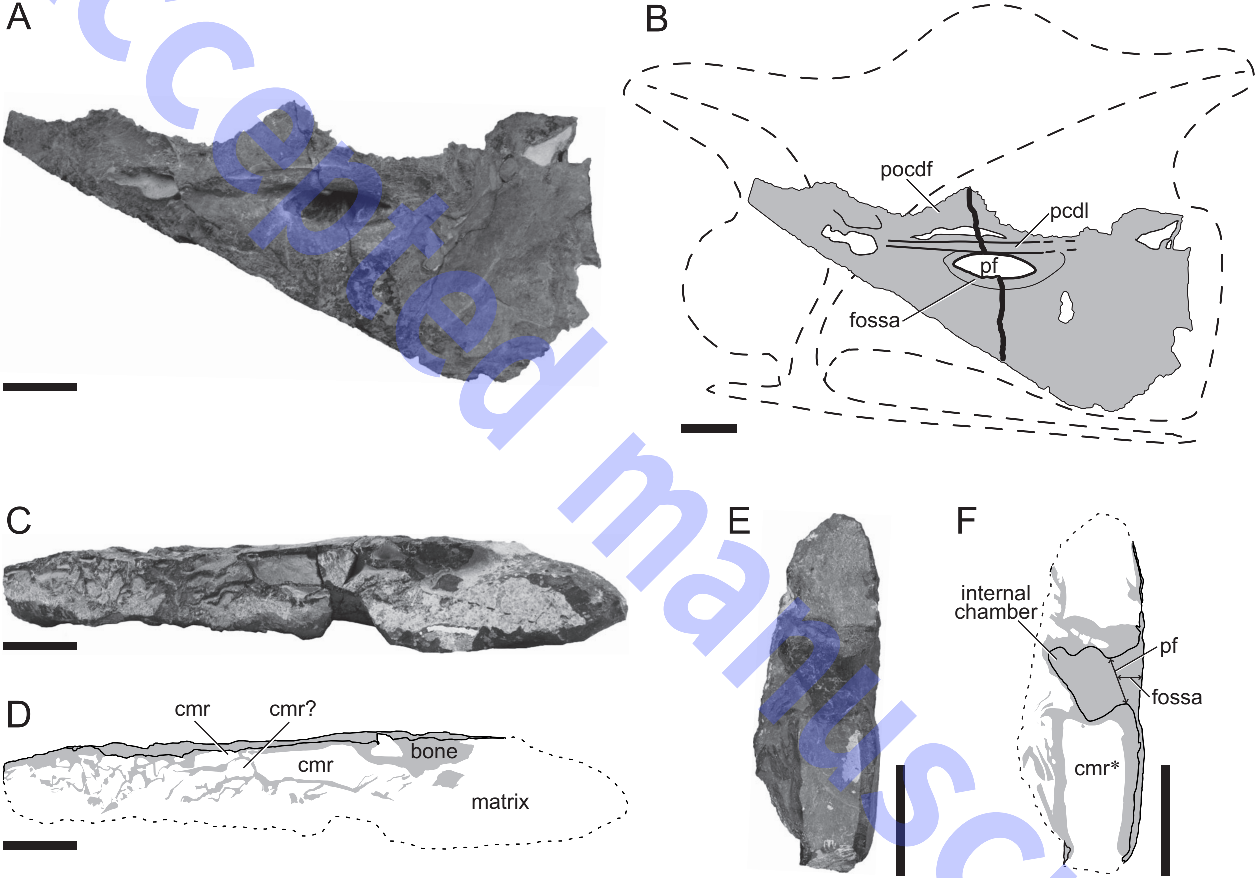
Figure 3. Computed tomography (CT) images of KMNH VP 600014. **A**, lateral view of the studied specimen indicating the sections at which CT images were obtained; **B**, CT

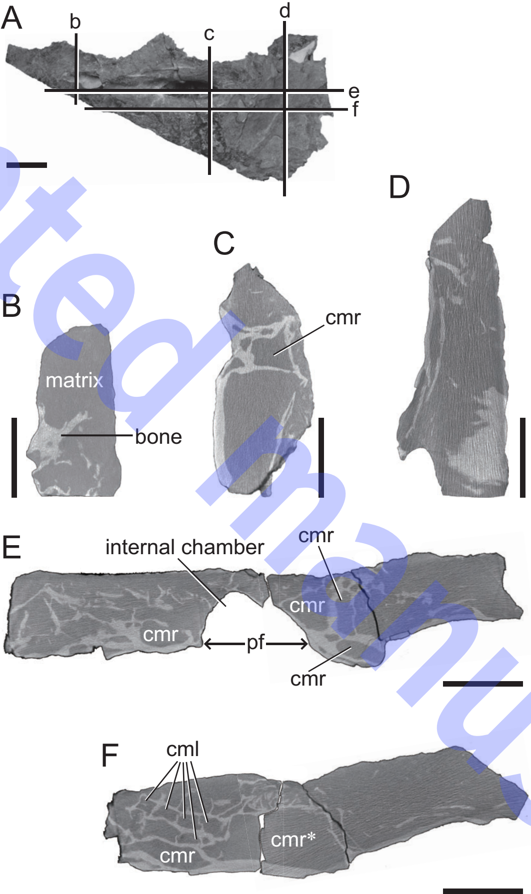
image at section b in A; **C**, CT image at section c in A; **D**, CT image at section d in A; **E**, CT image at section e in A; **F**, CT image at section f in A with the largest camera in this specimen labeled “cmr*”. Anterior: to the left in A, E, F; dorsal: to the top in A–D; lateral: to the left in B–D and to the bottom in E, F. Scale bars: 5 cm.

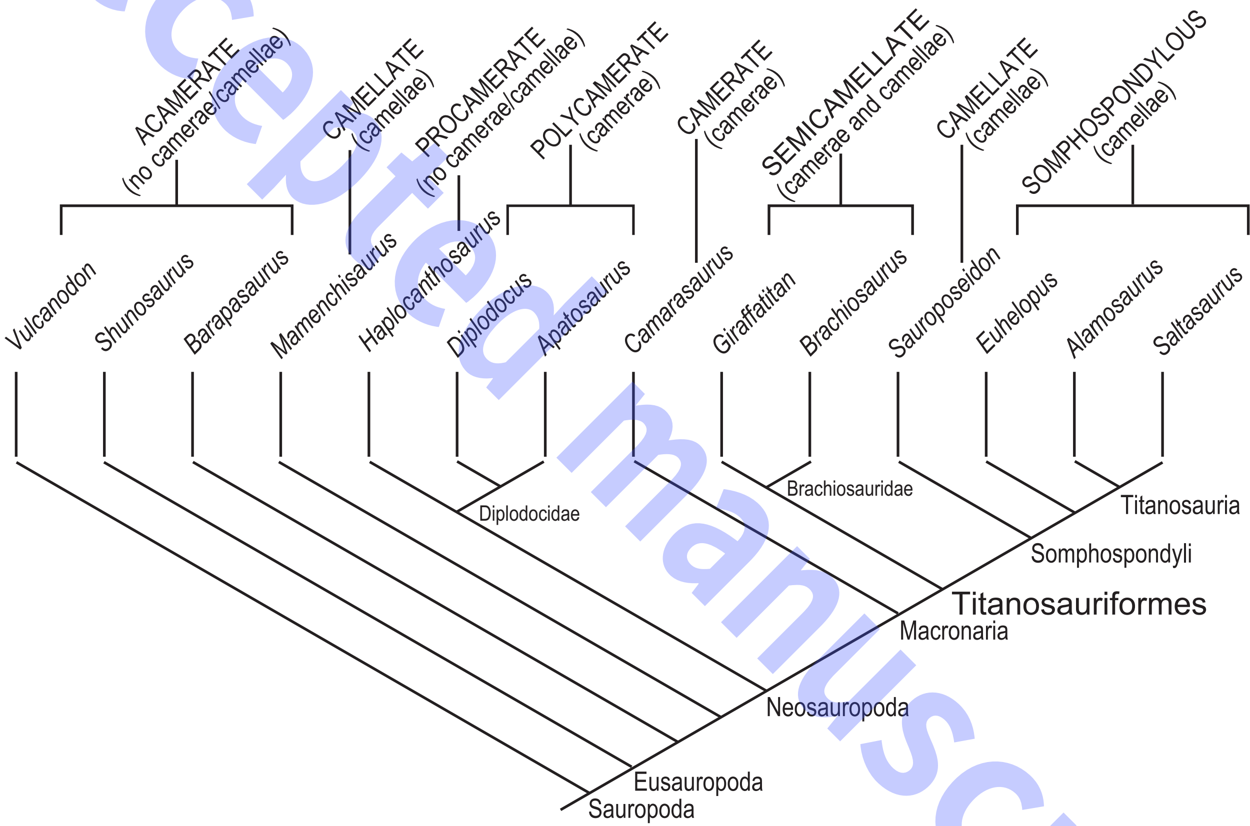
Figure 4. Vertebral pneumaticity of sauropods. Classification of vertebrae based on pneumatic characters proposed by Britt (1993, 1997) and Wedel *et al.* (2000a) is shown at the top in upper case. Modified after Wedel (2003), Ksepka and Norell (2010) and D'Emic (2012).

Table 1. List of titanosauriform specimens from the Cretaceous in Japan. Abbreviations: Fm, Formation, Gp, Group.


A
132°
136°
140°
144°E
44°N
40°
36°
Hokkaido
JAPAN
Honshu
Kyushu
Shikoku
Legend
Shimonoseki Subgroup
Wakino Subgroup
fault
anticlinal axis
synclinal axis
N
Yamaguchi Prefecture
Shimonoseki
Kitakyushu
Onga River
Locality
33°45′ N
Nakama
Kokura area
Nogata
Fukuoka Prefecture
0
10 km
130°30′
Wakino area
130°45′
131°E
B
Shimonoseki Subgroup
Kumagai Fm
Gamo Fm
Takatsuo Fm
Dobaru Fm
Kanmon Group
Wakino Subgroup
Yobuno Group (Paleozoic)
200 m
100
0
KMNH VP 600014
Legend
mudstone
alternation of mudstone and sandstone
sandstone
conglomerate
tuff
horizon of fossil occurrence


A
B
pocdf
pcdl
pf
fossa
C
D
cmr
cmr?
bone
cmr
matrix
E
F
internal chamber
pf
fossa
cmr*


A
b
c
d
e
f
B
matrix
bone
C
cmr
D
E
internal chamber
cmr
cmr
cmr
pf
cmr
cmr
F
cml
cmr
cmr*


ACAMERATE
(no camerae/camellae)
CAMELLATE
(camellae)
PROCAMERATE
(no camerae/camellae)
POLYCAMERATE
(camerae)
CAMERATE
(camerae)
SEMICAMELLATE
(camerae and camellae)
CAMELLATE
(camellae)
SOMPHOSPONDYLOUS
(camellae)
Vulcanodon
Shunosaurus
Barapasaurus
Mamenchisaurus
Haplocanthosaurus
Diplodocus
Apatosaurus
Camarasaurus
Giraffatitan
Brachiosaurus
Sauroposeidon
Euhelopus
Alamosaurus
Saltasaurus
Diplodocidae
Brachiosauridae
Titanosauria
Somphospondyli
Titanosauriformes
Macronaria
Neosauropoda
Eusauropoda
Sauropoda

Taxon	Horizon	Geological age (reference)	Elements	Reference for taxon
Titanosauriformes	Tamayama Fm, Futaba Gp	Coniacian (Saegusa and Tomida, 2011)	teeth	Saegusa and Tomida (2011)
Tambatitanis amicitiae	"Lower Fm", Sasayama Gp	Albian (Kusuhashi *et al*., 2013)	partial skeleton	Saegusa and Ikeda (2014)
Titanosauriformes	Gamo Fm, Kanmon Gp	Albian (Miyazaki *et al*., 2019)	cervical vertebra	this study
Fukuititan nipponensis	Kitadani Fm, Tetori Gp	Aptian (Fujita, 2003)	partial skeleton	Azuma and Shibata (2010)
Titanosauriformes	Kuwajima Fm, Tetori Gp	Barremian - Aptian (Matsuoka *et al*., 2016)	teeth	Barrett *et al*. (2002)
Titanosauriformes	Sebayashi Fm, Sanchu Gp	Barremian (Terabe *et al*., 2007)	tooth	Takakuwa *et al*. (2008)
Titanosauriformes	Tatsukawa Fm, Monobegawa Gp	Hauterivian - Barremian (Matsukawa and Ito, 1995)	tooth	Tsujino *et al*. (2020)
Titanosauriformes	Matsuo Gp	Valanginian - Barremian (Kawabata, 2001)	partial skeleton	Tomida and Tsumura (2006)