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A hadrosauroid vertebra from the Upper Cretaceous Izumi Group, Kagawa Prefecture, Japan

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Abstract. Of the four main Japanese islands, Late Cretaceous dinosaur fossils have been discovered in Hokkaido, Honshu, and Kyushu. Here, we report the first Late Cretaceous dinosaur from the remaining main island Shikoku, an isolated dorsal vertebra from the upper Campanian Hiketa Formation (Izumi Group) in Sanuki, Kagawa Prefecture. The vertebra is incomplete, comprising a robust centrum with a subrectangular profile that is generally characteristic of dinosaurs. Histological examination of the centrum reveals moderately packed trabecular bone and the complete absence of pneumatic structures, which precludes referral of the specimen to Saurischia or Pterosauria. Instead, we interpret it as a hadrosauriform ornithischian based on the slightly expanded anterior articular surface of the centrum; heart-shaped outline of the intervertebral surface, resulting from its dorsally wide and ventrally narrow shape; ventral keel; and neural canal partially embedded into the centrum. As the ventral positioning of the neural canal is common to *Bactrosaurus* and higher taxa within Hadrosauriformes, we tentatively refer the specimen to Hadrosauroidea. This discovery provides additional evidence that hadrosauriforms had dispersed into present-day Japan by the Campanian and highlights the potential of the Hiketa Formation to provide additional evidence to improve our understanding of the dinosaur diversity at the extreme eastern continental margin of Eurasia.

Keywords: hadrosauroid dinosaur, Hiketa Formation, Late Cretaceous, Shikoku, vertebra

Introduction

The number of Late Cretaceous dinosaur discoveries in Japan has increased steadily in recent decades (Shibata *et al*., 2017; Kubota, 2017), most of which have been derived from marine deposits (e.g. Hayakawa *et al*., 2005; Ohashi *et al*., 2015; Kobayashi *et al*., 2019). One such sequence of marine strata is the Upper Cretaceous Izumi Group, which is distributed across Shikoku, Awaji Island, and the Kii Peninsula in southwestern Japan. The Izumi Group preserves one of the largest and most taxonomically diverse assemblages of Late Cretaceous fossil vertebrates in Japan, mostly comprising marine reptiles and fish (Sato *et al*., 2012; Hara *et al*., 2018), but rare washed-in nonmarine vertebrates have also been discovered (Kobayashi *et al*., 2021). The upper Campanian Hiketa Formation of the Izumi Group has yielded marine vertebrate fossils such as fishes, turtles, mosasaurs, and a plesiosaur (Tanimoto and Kanazawa, 2001; Tanimoto, 2005), but no terrestrial vertebrates have been reported to date. Late Campanian vertebrate fossils are scarce in eastern Asia, so the vertebrate fossil record of the Hiketa

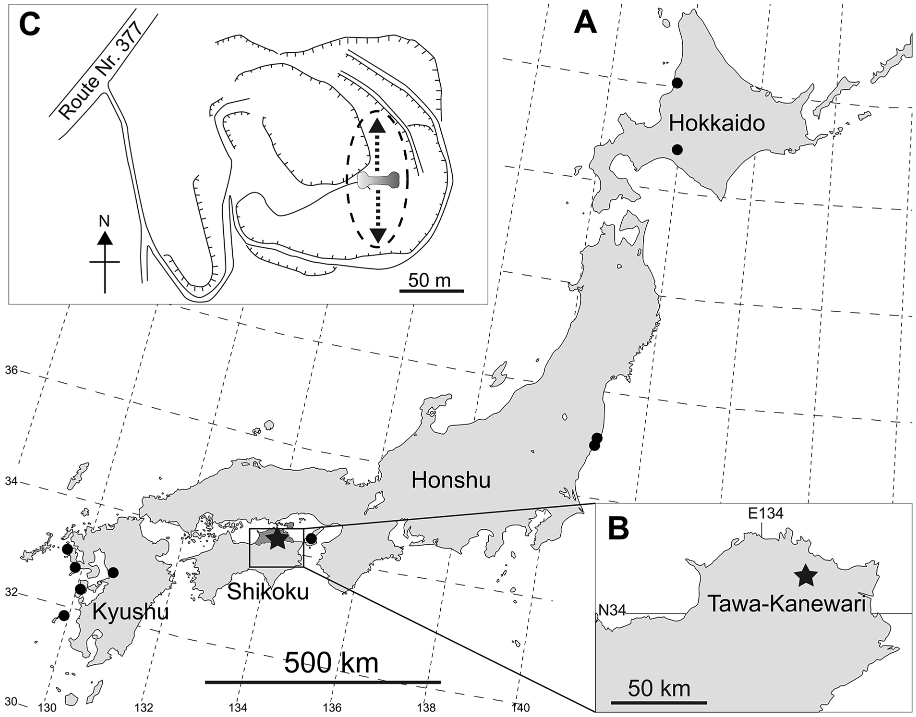

Figure 1. Locality map of OMNH MV-94. **A,** maps showing the locality of the studied sample OMNH MV-94 (black star) and other Late Cretaceous hadrosauroids (black circles); **B,** location of the Tawa Rock Quarry within Kagawa, Japan; **C,** schematic map of the Tawa Rock Quarry, modified from Tsujino (2004). The dotted circle in C indicates the location where OMNH MV-94 was discovered within the quarry.

Formation has helped elucidate Campanian marine vertebrate diversity in the northwestern Pacific (Hara *et al*., 2018). In contrast, late Campanian terrestrial vertebrate paleoecology in the easternmost part of Asia has remained unclear. Here, we describe the first terrestrial vertebrate fossil from the Campanian Hiketa Formation, a partial isolated dorsal vertebra from a dinosaur.

Geological setting

This dinosaur vertebra (OMNH MV-94) was discovered at Tawa Rock Quarry (*Tawa Saisekijo*) in Tawa-Kanewari, Sanuki, Kagawa Prefecture, Japan (Figure 1). It was retrieved from a float block that had been dislodged during commercial quarrying activities. This block is associated with a black siltstone bed intercalated with turbidite sandstones, previously described as “Facies C” of the Hiketa Formation by Tsujino (2004); however, it is not precisely known from which horizon of the bed it originated. The age of the Hiketa Formation is considered as the late Campanian based on the occurrence of the ammonoid *Baculites kotanii* (Morozumi, 1985).

Material and methods

An isolated dorsal vertebra OMNH MV-94 was discovered in 1986 by one of the authors of this paper (Y. K.), and it is reposited at the Osaka Museum of Natural History. To study its internal morphology and microanatomy, X-ray computed tomography (CT) scan data were acquired using a Nikon XTH-320 microfocus CT inspection system at Nikon Solutions Co., Ltd., Kanagawa, Japan. Scans were obtained with a voxel size of 59.1 µm at a voltage of 320 kV and current of 360 µA.

Additionally, an indeterminate hadrosaurid dorsal vertebra (MPC-D-100/770) from the Upper Cretaceous Baynshire Formation of Mongolia was CT scanned for comparison. This specimen was scanned using a Latheta LCT-200 micro-CT scanner (Hitachi Aloka Medical, Ltd., Tokyo, Japan) at the Okayama University of Science with a voxel size of 230 µm at a voltage of 80 kV and a current of 200 µA.

OMNH MV-94 was compared to the vertebrae of a diversity of ornithischian dinosaurs. Comparisons to *Scolosaurus cutleri* (NSM PV-20381), *Protoceratops andrewsi* (MPC-D 100/530), *Gobihadros mongoliensis* (MPC-D 100/746) and *Corythosaurus* sp. (OUSM-FV-001) were based on firsthand observations of speci-

Table 1. List of the comparative anterior dorsal vertebrae referenced in this study. Shaded areas highlight features that are shared with OMNH MV-94. Specimens observed firsthand are denoted by an asterisk.

Referred taxon		Anterior surface	Widest position	Ventral keel	Neural canal	Lateral concavity	Anteroposterior compression	Reference
OMNH MV-94	–	Convex	Dorsal end	Present	Embed in centrum	Shallow	Absent	This study *
Ankylosauria	*Euoplocephalus tutus*	Flat or concave	Middle	Absent	Dorsal to centrum	Deep	Absent	Arbour and Currie, 2013
	Pinacosaurus grangeri	Flat or concave	Middle	Absent	Dorsal to centrum	Deep	Absent	Burns *et al.*, 2015
	Scolosaurus cutleri	Flat or concave	Middle	Absent	Dorsal to centrum	Deep	Absent	NSM PV-20381 *
Pachycephalosauria	*Homalocephale calathocercos*	Flat or concave	Middle/Dorsal	Present/ Absent	Dorsal to centrum	Shallow	Absent	Maryańska and Osmólska, 1974
	Stegoceras validum	Flat or concave	Dorsal	Absent	Embed?	Shallow	Absent	Gilmore, 1924
Ceratopsidae	*Chasmosaurus belli*	Flat or concave	Middle/Ventral	Absent	Dorsal to centrum	Shallow	Present	Maidment and Barrett, 2011
	Centrosaurus apertus	Flat or concave	Middle/Ventral	Absent	Dorsal to centrum	Shallow	Present	Brown, 1917; Lull, 1933
	Protoceratops andrewsi	Flat or concave	Middle	Absent	Dorsal to centrum	Shallow	Absent	Brown and Schlaikjer, 1940; MPC 100/530 *
	Styracosaurus albertensis	Flat or concave	Middle/Ventral	Absent	Dorsal to centrum	Shallow	Present	Holmes and Ryan, 2013
	Triceratops prorsus	Flat or concave	Middle/Ventral	Absent	Dorsal to centrum	Shallow	Present	Hatcher *et al.*, 1907
Basal ornithopoda	*Parksosaurus warreni*	Concave	Middle	Present	Dorsal to centrum	Shallow	Present	Sues *et al.*, 2023
	Mochlodon vorosi	Flat or concave	Middle	Present	Dorsal to centrum	Shallow	Absent	Ősi *et al.*, 2012
	Zalmoxes robustus	Flat	Middle	Present	Dorsal to centrum	Shallow	Absent	Weishampel *et al.*, 2003
	Dryosaurus altus	Flat	Middle	Absent	Dorsal to centrum	Shallow	Absent	Galton, 1981
	Cumnoria prestwichii	Flat	Dorsal end	Absent	Dorsal to centrum	Shallow	Absent	Maidment *et al.*, 2022
	Camptosaurus aphanoecetes	Flat or convex	Dorsal end	Present	Dorsal to centrum	Shallow	Absent	Carpenter and Wilson, 2008
Hadrosauriformes	*Iguanodon bernissartensis*	Convex	Dorsal end	Present	Dorsal to centrum	Shallow	Absent	Norman, 1980
	Equijubus normani	Convex	Dorsal end	Present	Dorsal to centrum	Shallow	Absent	You *et al.*, 2003
	Eolambia caroljonesa	Convex	Dorsal end	Present	Dorsal to centrum	Shallow	Absent	McDonald *et al.*, 2012, 2017
	Bactrosaurus johnsoni	Convex	Dorsal end	Present	Embed	Shallow	Absent	Gilmore, 1933; Godefroit *et al.*, 1998
	Gilmoreosaurus mongoliensis	Convex	Dorsal end	Present	Embed	Shallow	Absent	Prieto-Márquez and Norell, 2010
	Gobihadros mongoliensis	Convex	Dorsal end	Present	Embed	Shallow	Absent	Tsogtbaatar *et al.*, 2019; MPC-D 100/746 *
	Probrachylophosaurus bergei	Convex	Dorsal end	Present	Dorsal to centrum	Shallow	Absent	Freedman Fowler and Horner, 2015
	Brachylophosaurus canadensis	Convex	Dorsal end	Present	Embed	Shallow	Absent	Prieto-Márquez, 2007
	Kritosaurus navajovius	Convex	Dorsal end	Present	Embed	Shallow	Absent	Lull and Wright, 1942
	Secernosaurus koerneri	Convex	Dorsal end	Present	Embed	Shallow	Absent	Prieto-Márquez and Salinas, 2010
	Kamuysaurus japonicus	Convex	Dorsal end	Present	Embed	Shallow	Absent	Kobayashi *et al.*, 2019
	Edmontosaurus regalis	Convex	Dorsal end	Present	Embed	Shallow	Absent	Campione, 2014
	Nipponosaurus sachalinensis	Convex	Dorsal end	Present	Embed	Shallow	Absent	Suzuki *et al.*, 2004
	Parasaurolophus cyrtocristatus	Convex	Dorsal end	Present	Embed	Shallow	Absent	Ostrom, 1963
	Olorotitan arharensis	Convex	Dorsal end	Present	Embed	Shallow	Absent	Godefroit *et al.*, 2012
	Amurosaurus riabinini	Convex	Dorsal end	Present	Embed/Dorsal	Shallow	Absent	Godefroit *et al.*, 2004
	Magnapaulia laticaudus	Convex	Dorsal end	Present	Embed	Shallow	Absent	Prieto-Márquez *et al.*, 2012
	Corythosaurus sp.	Convex	Dorsal end	Present	Embed	Shallow	Absent	OUSM-FV-001 *

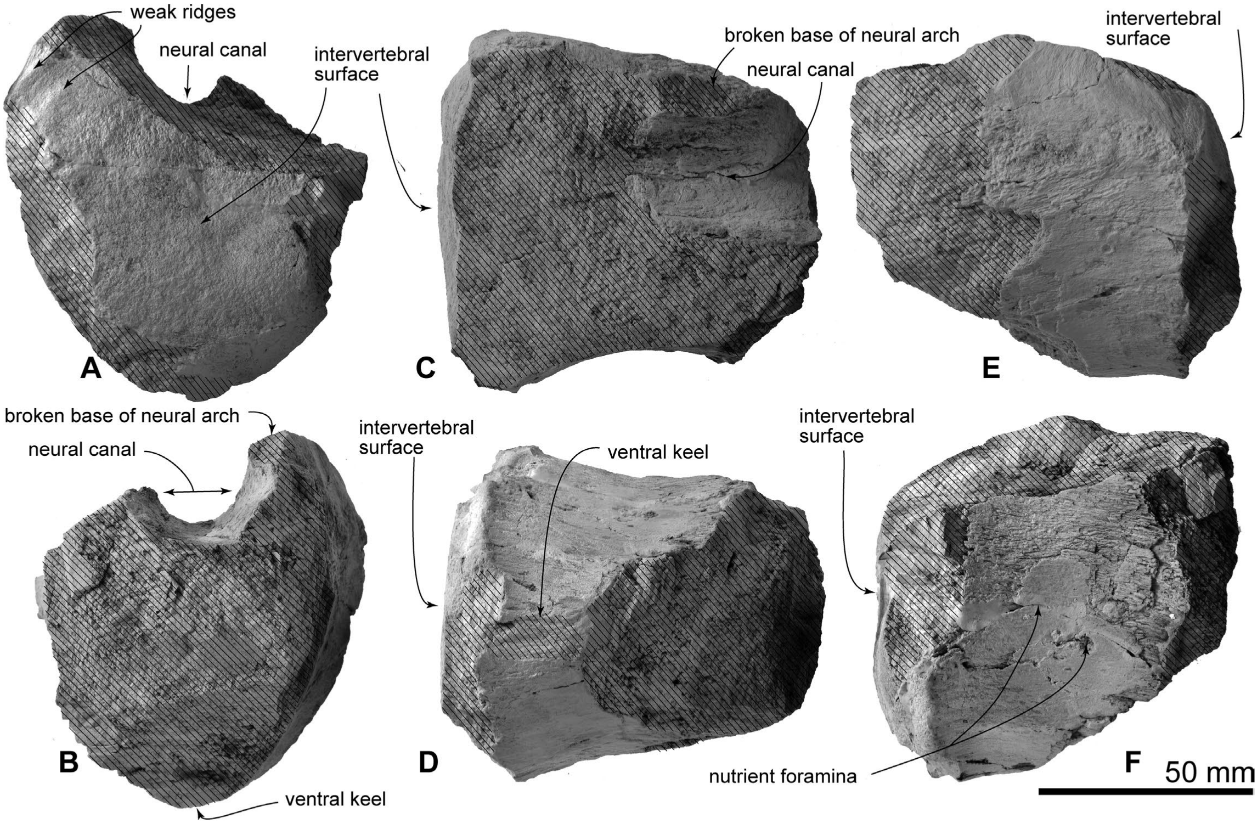

Figure 2. Photographs showing various views of the dorsal vertebra OMNH MV-94. **A,** anterior view; **B,** posterior view; **C,** dorsal view; **D,** ventral view; **E,** right lateral view; **F,** left lateral view. Diagonal line areas indicated damaged regions.

mens. All other comparisons were based on data gathered from existing literature, as summarized in Table 1.

Institutional abbreviations.—MPC-D, Mongolian Paleontology Collection–Dinosaur, Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; NSM, National Museum of Nature and Science, Tokyo, Japan; OMNH, Osaka Museum of Natural History, Osaka, Japan; OUSM-FV, Okayama University of Science, Museum of Dinosaur Research, fossil vertebrate collection, Okayama, Japan.

Systematic paleontology

Dinosauria Owen, 1842 *sensu* Langer *et al.*, 2020
Ornithischia Seeley, 1888 *sensu* Baron *et al.*, 2017
Cerapoda Sereno, 1986 *sensu* Madzia *et al.*, 2021
Ornithopoda Marsh, 1881 *sensu* Madzia *et al.*, 2021
Iguanodontia Baur, 1891 *sensu* Madzia *et al.*, 2021
Hadrosauroidea Huene, 1952 *sensu* Madzia *et al.*, 2021
Hadrosauroidea gen. *et* sp. indet.

Figure 2

Referred specimen.—OMNH MV-94, a partial isolated dorsal vertebra.

Locality.—Tawa Rock Quarry (*Tawa Saisekijo*) in Tawa-Kanewari, Sanuki City, Kagawa Prefecture, Japan.

Horizon.—Hiketa Formation, Izumi Group, upper Campanian (Tsujino, 2004; Misaki and Tsujino, 2021).

Description and comparison.—OMNH MV-94 preserves most of the centrum and the base of the associated right pedicle (Figure 2). It is interpreted as a dorsal vertebra based on the apparent absence of parapophyses or chevron facets. The pedicle is 15 mm thick, and the closure of the neurocentral suture cannot be confirmed externally or internally. The anterior articular surface is damaged along its circumferential margins but maintains some of its original structure. Weak ridges along the right dorsolateral and left ventrolateral margins of the anterior surface of the centrum give it a slightly convex anterior articular surface (Figure 2A, F). The centrum is wide dorsally and keeled ventrally, and the ventral margin of the neural canal is embedded deeply into the dorsal centrum (Figure 2A, B). This feature results in a dorsoventrally elongated appearance, in contrast to the subcircular-to-dorsoventrally short centra observed in large Late Cretaceous marine reptiles, such as plesiosaurs, mosasaurs,

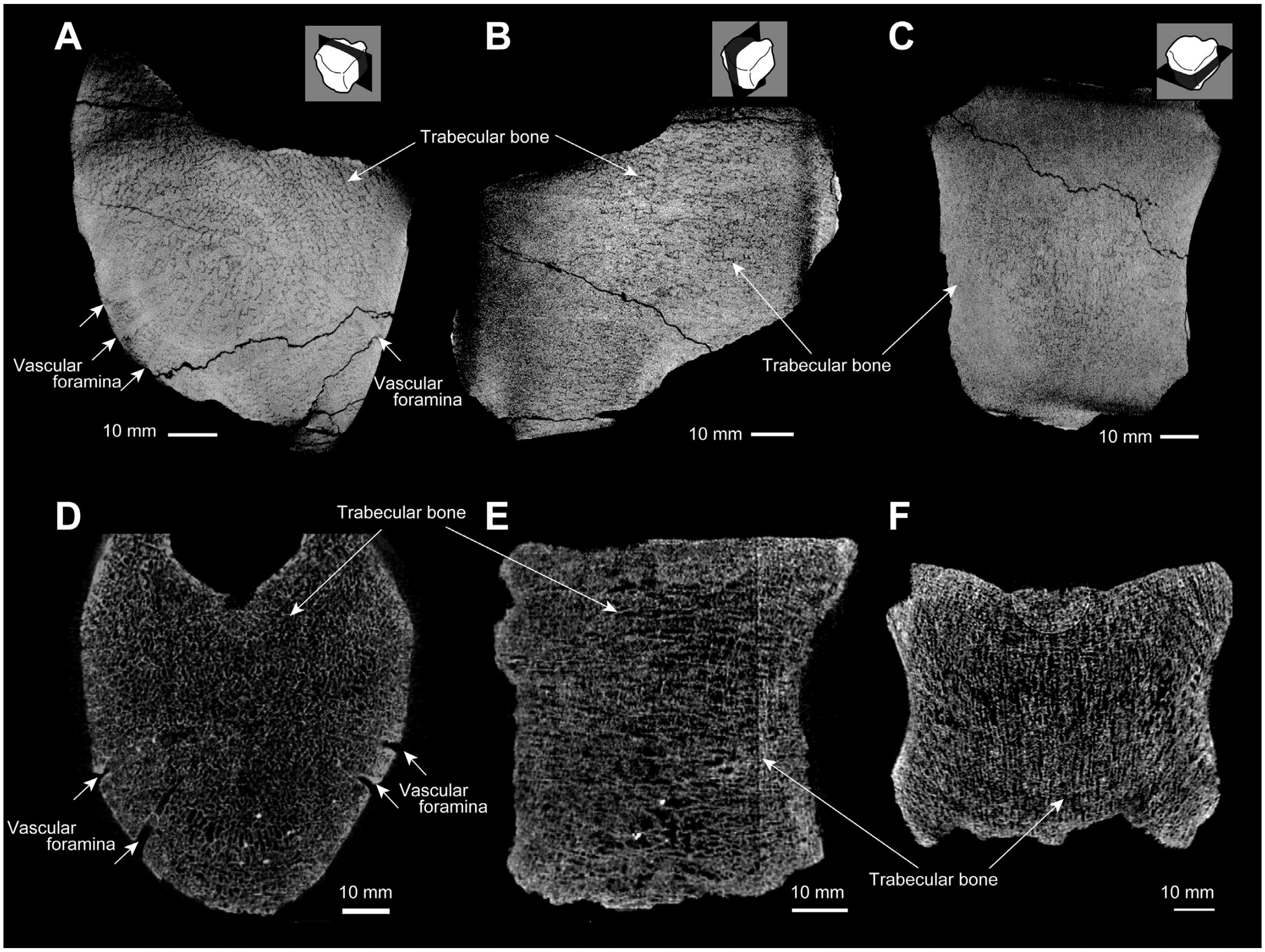

Figure 3. CT images of the dorsal vertebra of OMNH MV-94 (**A–C**) and a hadrosaurid MPC-D-100/770 from the Late Cretaceous Baynshire Formation of Mongolia (**D–F**). A, D, coronal sections; B, E, sagittal sections; C, F, horizontal sections.

turtles (Holmes, 1996; Sato *et al*., 2006, 2018; Lindgren *et al*., 2007; Nakajima *et al*., 2011) or crocodilians (Holland, 1909; Cossette and Brochu, 2020).

CT data reveal that the internal region of OMNH MV-94 is characterized by spongy bone devoid of pneumatic and/or large cavities, with a tight trabecular network and numerous intertrabecular spaces (Figure 3A–C). These characteristics are similar to those found in the hadrosaurid MPC-D 100/770 (Figure 3D–F) and differ from pterosaurs and saurischian dinosaurs in lacking vertebral pneumaticity. We instead tentatively identify it as the vertebra of an ornithischian dinosaur and hereafter restrict further comparisons to ornithischian taxa.

Among ornithischian dinosaurs, the apparent convexity of the anterior articular surface of the centrum is shared with hadrosauriforms (Norman, 1980; You *et al*., 2003) but not ankylosaurians, ceratopsids, pachycephalosaurs, or non-hadrosauriform ornithopods, which are generally amphiplatian or amphicoelous (Table 1; Dodson *et al*., 2004; Maryańska *et al*., 2004; Vickaryous *et al*., 2004; Ősi *et al*., 2012). The anterior convexity is prominent on the ventral half of the centrum, whereas the dorsal half appears to be nearly flat, as in some anterior dorsal centra of *Equijubus* (You *et al*., 2003). The transverse width of the centrum is greater dorsally than ventrally (Table 2), and the ventral margin appears to be weakly keeled, although the surface is slightly damaged. Although the neural canal region is broken off and missing from the anterior half, the posterior half demonstrates that the neural canal is partially embedded in the centrum (Figure 2A–C). The dorsoventrally tall and ventrally tapering shape of the intervertebral surface is similar to the condition in several hadrosauriforms (e.g. *Edmontosaurus*: Campione, 2014). In contrast, the intervertebral surfaces of the dorsal centra are subcircular or pear-shaped in Late Cretaceous ceratopsians (Dodson *et al*., 2004) and sub-

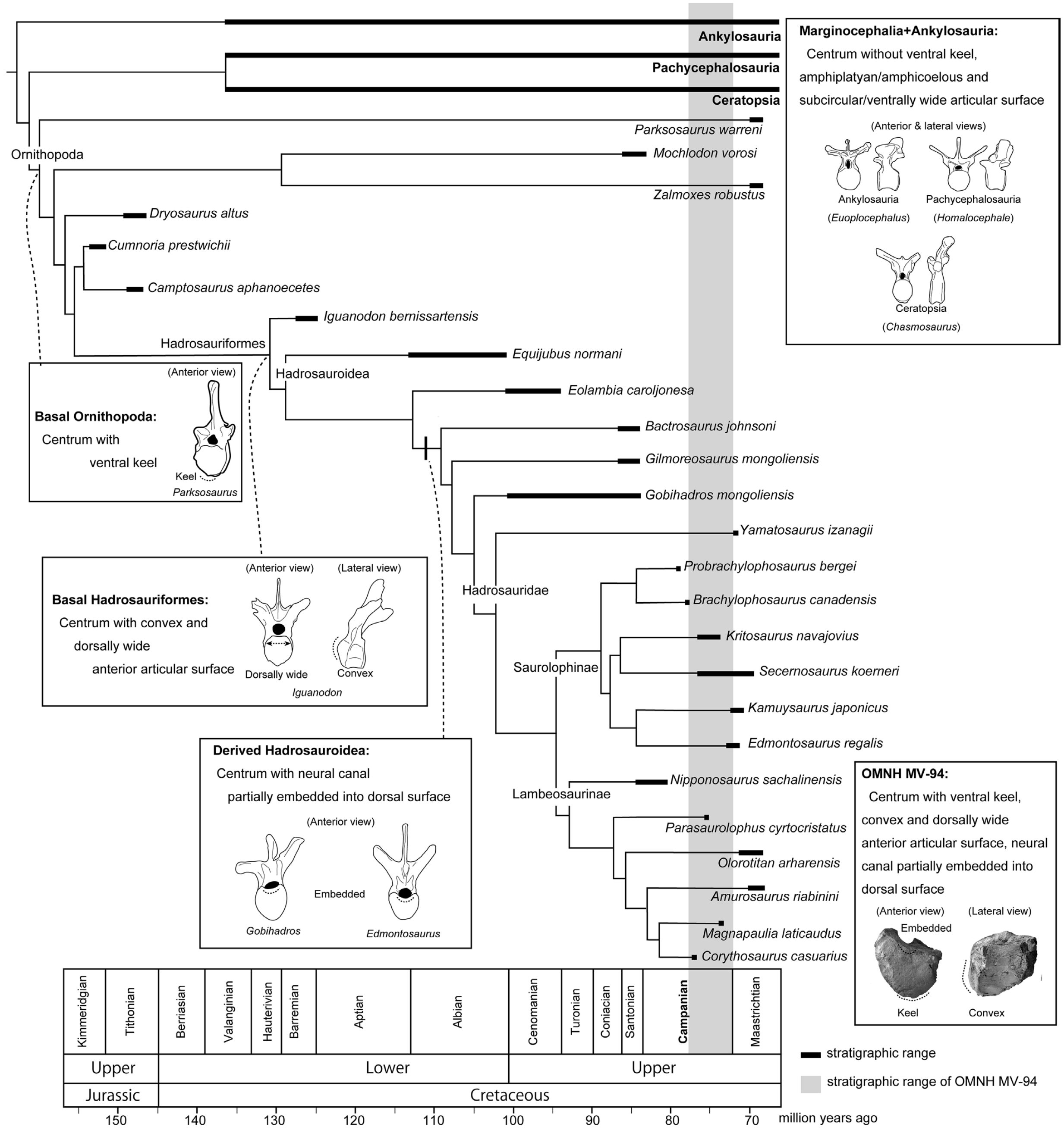

Figure 4. Morphological features of anterior dorsal vertebra mapped onto the phylogeny of Hadrosauriformes. The modified phylogenetic tree is based on Ősi *et al.* (2012), Slowiak *et al.* (2020) and Kobayashi *et al.* (2021). Note that not all taxa are preserved with dorsal vertebrate (e.g. *Yamatosaurus*). The shaded area shows the stratigraphic range of OMNH MV-94.

circular in Late Cretaceous ankylosaurians (Vickaryous *et al.*, 2004) and basal ornithopods (Weishampel *et al.*, 2003; Ősi *et al.*, 2012; Sues *et al.*, 2023) in both anterior and posterior views. OMNH MV-94 also differs from the pachycephalosaurs *Stegoceras* in the presence of a ventral keel (Gilmore, 1924), and *Homalocephale* (Maryańska and Osmólska, 1974) and non-hadrosauriform basal iguanodontians (*Dryosaurus* [Galton, 1981], *Cumnoria* [Maidment *et al.*, 2022], *Camptosaurus* [Carpenter and Wilson, 2008]) in the embedded neural canal. The lateral surface of the dorsal vertebra is slightly concave anteroposteriorly and is pierced by at least four small (< 5 mm) vascular foramina (Figures 2F, 3A). The concavity is weak, and the anterior margin does not flare lat-

Table 2. Linear measurements of OMNH MV-94. Parameters are measured in either the transverse or dorso-ventral dimensions.

Element	Measurement (mm)
Maximum anteroposterior length of the centrum	98.5
Maximum dorsoventral height of the centrum	83
Minimum transverse width of the middle of the centrum	65.2
Maximum transverse width of the centrum	92

erally, unlike in ankylosaurids, which have spool-shaped dorsal centra (Arbour and Currie, 2013). The centrum is much longer than tall (Table 2), similar to the anterior and middle dorsal centra of hadrosauriforms (Campione, 2014), pachycephalosaurs (Gilmore, 1924; Maryańska and Osmólska, 1974) and non-hadrosauriform ornithopods (Galton, 1981; Carpenter and Wilson, 2008), and differing from the disc-shaped dorsal centra of ceratopsians (Dodson *et al.*, 2004). The anterodorsal and the posteroventral regions are severely damaged and thus anatomically uninformative. Comparing OMNH MV-94 to pachycephalosaurs is difficult owing to the limited availability of pachycephalosaur dorsal vertebrae, but it differs from all described pachycephalosaur dorsal vertebrae in its convex anterior articular surface (*Homalocephale*: Maryańska and Smólska, 1974; *Stegoceras*: Gilmore, 1924). OMNH MV-94 is also much larger than the dorsal vertebrae of all currently known pachycephalosaurs (Table 1). OMNN MV-94 share a character with basal ornithopods and non-hadrosauriform basal iguanodontins, which is ventrally keeled centrum and/or slightly convex articular surface (Table 1), but it differs in having the embedded neural canal into the dorsal surface of the centrum. Based on these comparisons, we identify OMNH MV-94 as a hadrosauriform dorsal vertebra.

Evaluating the taxonomy of OMNH MV-94 is challenging to determine owing to the wide variation in dorsal centrum morphology within Hadrosauriformes. This variation includes changes in shape along the axial series of a single individual and interspecific variations. One example of interspecific variation is the ventral keel. Although the ventral keel was used to identify OMNH MV-94 as a hadrosauriform, it is occasionally lost secondarily in both basal and derived forms (e.g. *Eolambia*: McDonald *et al.*, 2012; *Probrachylophosaurus*: Freedman Fowler and Horner, 2015). Within a single individual, hadrosauriform dorsal centra transition from elongated opisthocoelous to short amphiplatyan centra from anterior to posterior. The degree of anterior expansion also varies among species, with anteriorly convex centra limited to the anteriormost two or three dorsal centra in basal hadrosauriforms (e.g. *Equijubus*: You *et al.*, 2003; *Gobihadros*: Tsogtbaatar *et al.*, 2019) and extending to the seventh (*Edmontosaurus*: Campione, 2014) or 12th (*Parasaurolophus*: Ostrom, 1963) dorsal centra in derived forms. Although the degree of anteroposterior elongation varies, all hadrosauriform anterior and middle dorsal centra (up to approximately the 12th) referenced herein are longer than tall, so we interpret OMNH MV-94 as an anterior or middle dorsal vertebra.

The position of the neural canal also varies within an individual. The canal tends to be more deeply embedded into the dorsal surface of the centrum in anterior dorsal vertebrae than in posterior ones. At the same time, the neural canal position shows some degree of phylogenetic signal (Figure 4). The neural canal of the anterior and mid-dorsal centra is less deeply embedded into the dorsal surface of the centrum in basal hadrosauriforms such as *Iguanodon* (Norman, 1980) and *Eolambia* (McDonald *et al.*, 2012) than in *Bactrosaurus* (Godefroit *et al.*, 1998), *Gilmoreosaurus* (Prieto-Márquez and Norell, 2010), *Gobihadros* (Tsogtbaatar *et al.*, 2019), and other derived taxa, although at least one exception exists (*Probrachylophosaurus*; Freedman Fowler and Horner, 2015). Therefore, although dorsal centra morphology is highly variable, the position of the neural canal suggests that OMNH MV-94 may belong to the hadrosauroid clade comprising *Bactrosaurus*, *Gilmoreosaurus*, *Gobihadros*, and Hadrosauridae.

Discussion

Although ornithopods are among the most abundant non-avian dinosaurs discovered in Japan, Campanian occurrences remain scarce, with reported finds limited to brief conference abstracts (Miyata *et al*., 2014; Shibata *et al*., 2014, 2022). OMNH MV-94 thus represents the first Campanian ornithopod dinosaur formally described from Japan. The global taxonomic diversity of hadrosauroids was relatively high during the Campanian, particularly in North America (Condamine *et al*., 2021), but the Asian record remains poor. Until now, the known Campanian record of Asian hadrosauroids was limited to China (*Shantungosaurus*: Xing *et al*., 2014; *Tsintaosaurus*: Prieto-Márquez and Wagner, 2013), Mongolia (*Plesiohadros*: Tsogtbaatar *et al*., 2014) and possibly Kazakhstan (*Aralosaurus*: Prieto-Márquez *et al*., 2013). OMNH MV-94 therefore extends the known geographic range of Hadrosauroidea at the end of the Campanian to the far eastern continental margin of Asia. Kobayashi *et al.* (2021) recently described the basal hadrosaurid *Yamatosaurus* from the lower Maastrichtian Kita-ama Formation of the

Izumi Group and proposed that this region of Japan could have been a refugium for basal forms at the end of the Cretaceous. Although the phylogeny of OMNH MV-94 and its relationship to *Yamatosaurus* cannot be rigorously evaluated given its incomplete nature, its apparent hadrosauroid affinities tentatively support the hypothesis that present-day Shikoku and southeastern Honshu may have been a refugium for basal hadrosauroids and encourages further investigation in this region.

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Author contributions

S. H. designed this research. Y. K. contributed to the geological aspect of this study. S. H., Y. N., Y. T., and B. T. B. analyzed the external morphological features. S. H., Y. N., and C. T. analyzed its CT data. Y. K. prepared the specimen. S. H., Y. N., Y. T., and B. T. B. wrote the paper.