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A basal mosasauroid from the Campanian (Upper Cretaceous) of Hokkaido, northern Japan

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Abstract:

A basal mosasauroid specimen, including a rib and a vertebra from middle to posterior portion of the trunk, is reported from the lower Campanian *Inoceramus (Platyceramus) japonicus* zone in Obira Town, northern Hokkaido, northern Japan. It is the second occurrence of basal mosasauroids sensu lato in Japan after the halisaurine *Phosphorosaurus ponpetelegans*, but represents a larger individual than the *P. ponpetelegans* holotype. The Obira specimen predates the early Maastrichtian *P. ponpetelegans* by about 10 million years, indicating colonization by basal mosasauroids of the northwestern Pacific by at latest the early Campanian age. While the overall morphology of the Obira specimen agrees well with that of a halisaurine vertebra, the presence of well-developed zygantra (zygosphenes missing postmortem if present) on the vertebra and its inclined condyle uniquely align the specimen with *Pannoniasaurus inexpectatus*, a Santonian-aged basal mosasauroid from freshwater deposits in Hungary.

Key words: Mosasauroidea, Halisaurinae, Tethysaurinae, lower Campanian

Introduction

The Mosasauroidea Camp, 1923 includes derived, often large-bodied hydropelvic and hydropedal genera such as mosasaurine *Mosasaurus* and tylosaurine *Tylosaurus*, as well as basal, plesiopelvic and plesiopedal members that are typically small-sized, such as *Aigialosaurus* and *Tethysaurus* (e.g., Bardet *et al.*, 2003; Bell and Polcyn, 2005; Palci *et al*,. 2013). When a global mosasauroid phylogeny is concerned, halisaurine mosasaurs, while both hydropelvic and hydropedal (e.g. Palci *et al.*, 2013), present a unique problem concerning their placement within mosasauroids, where there have been a wide range of hypotheses in the past decade in particular, including: a sister clade to an aigialosaur *Komensaurus*, nested within Mosasauridae (Bell and Polcyn, 2005); a sister clade to Mosasaurinae within Mosasauridae (Palci *et al.*, 2013); and forming a clade along with two plesiopelvic taxa outside of Mosasauridae (Dutchak and Caldwell, 2009). Bell (1997) established a basic framework of the mosasaur phylogeny in which the Natantia, then a major clade of derived mosasaurs consisting of two subclades, “Russellosaurinae” (Russellosaurina *sensu* Polcyn and Bell, 2005) and Mosasaurinae Gervais, 1852, were recognized. Since then, phylogenetic studies have yielded conflicting results regarding the relationship of basal mosasauroids to more derived taxa (e.g. Bardet *et al.*, 2005; Bell and Polcyn, 2005; Dutchak and Caldwell, 2009; Polcyn *et al.*, 2014). In this study, the term "basal mosasauroids" is used in a broad, non-monophyletic sense and refers to halisaurines and all the mosasauroid taxa exhibiting plesiopelvic and/or plesiopedal conditions, including the only plesiopedal mosasaurine *Dallasaurus turneri*.

Japanese Cretaceous marine sediments have yielded a large number of marine reptiles, including plesiosaurs, turtles, and mosasaurs (e.g., Sato *et al.*, 2012), making Japan one of the richest localities for Late Cretaceous marine reptiles in the circum-Pacific region. Thus far, Japanese mosasaur specimens identifiable at taxonomic ranks below the Mosasauridae have been assigned to either Mosasaurinae (e.g. *Mosasaurus hobetsuensis* Suzuki, 1985; *M. prismaticus* Sakurai *et al.*, 1999) or Russellosaurina (e.g. *Taniwhasaurus mikasaensis* Caldwell *et al.*, 2008; *Tylosaurus* sp. in Chitoku, 1994). Remains of non-Natantian (*sensu* Bell 1997) mosasauroids were unknown until Konishi *et al.*, (2013, 2015) reported the occurrence of a partial skeleton of the halisaurine *Phosphorosaurus ponpetelegans* from the lowest Maastrichtian in Hobetsu, southern Hokkaido. In the present contribution, we describe a new basal mosasauroid specimen from the older Campanian strata in Obira, about 200 km north of Hobetsu, northern Hokkaido (Figure 1).

The new specimen consists of a partially damaged but uncrushed posterior dorsal vertebra, proximal end of a rib, and an unidentified bone fragment, and is housed in the Obira Town Board of Education in Rumoi County, Hokkaido, northern Japan. These bones were originally contained in a single calcareous nodule of approximately 150 mm diameter. According to the collector Mr. Tomizou Ishii of Asahikawa City, the nodule was collected in a small creek in the uppermost portion of Akano-sawa, a tributary of the Obirashibe River in the Tappu area of Obira Town (Figure 1). It was donated to the Obira Town Board of Education (OTBE) and given the specimen number Obr-3609. The nodule was mechanically and acid-prepared by one of us (TY) at Tokyo Gakugei University to extract the bones for this study.

Geological setting

The Cretaceous Yezo Group is widely distributed in the Tappu area, Obira Town, northern Hokkaido (Figure 1B, C). It has been studied by a number of authors (Tsushima *et al.*, 1958; Tanaka, 1963; Tanabe *et al.*, 1977; Funaki and Hirano, 2004; Oizumi *et al.*, 2005), and known to range from Albian to Campanian stages in this vicinity. Tanaka (1963) subdivided this group into 17 geological units, i.e., Ma to Ml and Ua to Ul. These geological subdivisions are widely applicable not only to the Tappu area, but also to the Kotanbetsu and Haboro areas to the north (e.g., Okamoto *et al.*, 2006; Tsujino and Maeda, 2007). In a recent scheme, the Yezo Group in the Tappu, Kotanbetsu, and Haboro areas is subdivided into Takimibashi, Tenkaritoge, Saku, and Haborogawa formations (Funaki and Hirano, 2004; Oizumi *et al.*, 2005).

A recent field survey by one of us (TN) in Akano-sawa Creek section in the Tappu area confirmed the presence of the Uk unit, i.e. the second uppermost geological unit of the Yezo Group in Tappu-Haboro area. It is the uppermost unit in the Cretaceous rocks exposed along Akano-sawa Creek, and correlates with the Hakobuchi Formation in southern Hokkaido, because of the similarity of lithofacies of the Uk unit and the base of the Hakobuchi Formation (basal member of "Hakobuchi Group" in Matsumoto, 1942) in the Hobetsu area, southern Hokkaido (TN pers. obs.).

OTBE Obr-3609 was collected as a float from locality 2 of the fifth (i.e., the northernmost) branch draining into the Akano-sawa Creek from the west (Figure 1D). In this section, an upper part of the Cretaceous Yezo Group and the Miocene Jugosensawa Formation are exposed with an unconformity in between (Figure 1E). Judging from the locality, original horizon of OTBE Obr-3609 is estimated to be an upper part of Ui-j or Uk unit of the Yezo Group. *Inoceramus* (*Platyceramus*) *japonicus* Nagao and

Matsumoto, 1940 (Figure 2A), an index inoceramid bivalve of the lowest Campanian (Toshimitsu *et al.*, 1995; Moriya *et al.*, 2001), occurs in Ui-j units of the Haboro, Kotanbetsu, and Tappu areas (Tanabe *et al.*, 1977; Oizumi *et al.*, 2005; Okamoto *et al.*, 2006). The same species occurs in Ui-j units at the Locality 1 (Figures 1E, 2A), and also from the second western branch (Oizumi *et al.*, 2005, figures. 4.3, 5F; Toshimitsu, 1988, figures. 15c, 25) of Akano-sawa Creek.

Upper parts of Uk unit in the Haboro and Kotanbetsu areas are correlated to the upper lower Campanian *Sphenoceramus orientalis*–*S. schmidti* inoceramid zone based on the occurrence of these species (Toshimitsu, 1988, Toshimitsu *et al.*, 1995). In the Uk unit in the Akano-sawa Creek section, we collected many *S. naumanni* (Yokoyama, 1989) (Figure 2C) and *Sphenoceramus* spp., but no index fossils of the upper lower Campanian have been found in our survey or in previous works. While absence of evidence is not necessarily evidence of absence, the conspicuous absence of *S. orientalis* indicates that the Uk unit in this area is likely lower than FAD of this species. Based on these biostratigraphic data, we conclude that the Ui-j and Uk units of Akano-sawa Creek that had yielded OTBE Obr-3609 belong to the lowest Campanian (ca. 83 Ma), *Inoceramus* (*Platyceramus*) *japonicus* zone, below *S. orientalis*–*S. schmidti* zone.

Institutional Abbreviations: HMG, Hobetsu Museum, Hokkaido, Japan; OTBE, Obira Town Board of Education, Hokkaido, Japan; YPM, Yale Peabody Museum, Connecticut, USA.

Systematic Paleontology

Squamata Oppel, 1811

Mosasauroidea Camp, 1923

Mosasauroidea gen. et sp. indet.

Figures 3–5

Referred specimen: OTBE Obr-3609. A posterior dorsal vertebra, an associated left posterior dorsal rib head, and unidentified bone fragment, all originally contained in a single calcareous nodule.

Description

The vertebra lacks anterior zygapophyses, left posterior zygapophysis, and most of the neural spine postmortem, and distal portions of the synapophyses are worn to various degrees; otherwise it is nearly complete and appears to be undeformed (Figures 3, 4). A major crack runs across the centrum, but as expected in a squamate vertebra, there are no traces of sutures between the centrum and the neural arch.

The centrum is distinctly procoelous and dorso-ventrally compressed (see Table 1 for the central measurements). The preserved portion of the cotyle on the anterior articular face of the centrum is oval, approximately 2.5 times as wide as it is high, and is smoothly concave. The damage to the anteroventral edge of the centrum appears minimal, suggesting that the anterior placement of synapophyses within the centrum is anatomically original, not preservational. The condyle of the centrum is an oval- to heart-shaped, with the height/width ratio of 0.69, and bears a few irregular small depressions that represent postmortem damage. The centrum width decrease constantly posteriorly with straight lateral margins, and the centrum is distinctly constricted immediately anterior to the condyle. Both conditions are present in *Pannoniasaurus* dorsal vertebrae, whereas a posterior cervical of a halisaurine *Phosphorosaurus* exhibits the former condition only (e.g. Makádi *et al.*, 2012: figure 6K; Konishi *et al.*, 2015: figure 17L). In addition, there is a shallow groove along the edge of the condyle on the ventral surface (Figures 3B, 4B). In profile, the condyle surface is tilted anterodorsally (Figure 3D).

The ventral surface is smooth and bears a very subtle ridge along the midline, but there is no sign of a discrete hypapophysis. At the anterolateral corner of the centrum, the synapophyses (or transverse processes) project laterally and slightly dorsally, so the centrum describes a short Y-shape in this aspect. Despite that both the synapophyses are damaged, the better-preserved left side clearly shows that the main body of the process is at the level of the neural arch, not the centrum (cf. Konishi *et al.*, 2015: figure 17M, N). Distally the end of the synapophysis widens dorsally, and the dorsolateral corner is smoothly rounded for rib articulation. In lateral view, the synapophysis is taller than wide, but the ventral extent of the rib facet cannot be exactly determined due to damage. Nevertheless, the ridge extending from the ventral border of the synapophysis to the lateroventral corners of the cotyle appears to have been present, and the ridge is confluent with the ventral border of the centrum.

On the anterolateral aspect of the synapophysis, a peculiar concave facet (“x” in Figure 3) exists on both sides. The texture of the facet differs from the rest of the cortical surface of the bone; it is smooth and lacks the compact bone layer, with numerous small pits (diameters of 2.5 mm to minute) distributing irregularly over the facet. A similar texture is commonly observed (but rarely described in literature) in the articular surfaces of plesiosaurian limb and girdle bones to suggest the presence of cartilage (e.g. Andrews 1910; Brown 1981; TS pers. obs.), whereas we are unaware of the presence of this texture in the corresponding regions of vertebra. The ventral edge of the facet is located slightly below the center of the cotyle but well above its ventral edge, whereas dorsally the facet extends beyond the base of the neural spine, situated approximately at the level of the zygantra. Considering the anatomical position, it is unlikely that this facet served as an articular facet for a skeletal—bony or cartilaginous—element, which would place it between adjacent ribs. The anterior surface of the synapophysis is distinctly concave and pitted in the dorsal vertebrae of the basal mosasauroid *Tethysaurus* and an unidentified pythonomorph (Bardet *et al.*, 2003: figure 2I; Houssaye, 2010: figures 2H, 3F, 3H); morphology and surface texture of these surfaces are not specifically mentioned in these authors' works, but the photographs show pitted concave surfaces of similar orientations. We suspect that the "facet x" in the Obira specimen actually represents a preservational aretefact, where such a concave surface has emerged as a result of the loss of the anterior zygapophyses, instead of it being a functional facet to receive another bone or a piece of cartilage. The lack of compact bone in the region, at present, cannot be accounted for.

The right postzygapophysis is nearly complete. The articular facet of the zygapophysis is 13 mm wide and 19 mm long, and is inclined at an angle of about 30 degrees from the horizontal plane. In posterior view, there is a pair of zygantra which consist of a pair of deeply excavated pits and nearly circular articular facets on the lateral wall of the pit (“ztaf” in Figure 4). The diameter of the facet is 12 mm, and it is oriented nearly vertical and slightly tilted dorso-posteriorly. Medial to the zygantra, one median (“mr” in Figure 4) and a pair of lateral ridges (“lr”: right one is broken) develop above the neural canal. The neural canal is slightly taller than wide, flat at the base and arched dorsally, and there is a median ridge on the floor but mostly obscured by the matrix.

The preserved proximal portion of a dorsal rib (Figure 5) is 55 mm long and includes the singular head. The rib facet is ovoid (19 mm wide and 35 mm tall) and slightly concave, and its size and morphology match the rib facet at the dorsolateral corner of the left synapophysis of the vertebra described above. The shaft narrows rapidly distally, and the maximum diameter is less than 20 mm (< 57%) at the broken distal end.

The unidentified bone fragment was preserved with the vertebra inside the nodule. It may represent a part of the missing neural spine, but its cortical bone is completely lost and cannot be identified with confidence.

Discussion

The clear lack of the hypapophysis and haemapophyses indicate that the vertebra of OTBE Obr-3609 is derived from a dorsal series. Dorsoventrally compressed dorsal centra are commonly known among basal mosasauroids *sensu lato* such as halisaurines, *Tethysaurus*, and *Pannoniasaurus* but not *Dallasaurus* (e.g., Lingham-Soliar, 1991; Holmes and Sues, 2000; Bardet *et al.*, 2003; Bardet *et al.*, 2005; Bell and Polcyn, 2005; Lindgren and Siverson, 2005; Makádi *et al.*, 2012; Konishi *et al.*, 2015), whereas those of more derived mosasauroids are transversally oval to circular (e.g., Russell, 1967). In addition, the remaining shaft of the associated dorsal rib readily converges distally, suggesting that the complete rib was short. Short dorsal ribs are limited to roughly the posterior one third of the dorsal series in primitive mosasauroids such as *Komensaurus* and *Carsosaurus* (e.g., Konishi *et al.*, 2012), *Pannoniasaurus* (Macádi *et al.*, 2012: figure 4), and in two halisaurine species *Eonatator sternbergii* and *E. coellensis* (Páramo-Fonseca, 2013; TK pers. obs.). Even though cervical ribs are also short, the synapophyses on cervical vertebrae in mosasauroids occur centrally or posteriorly on the lateral surface of centra, not anteriorly as in OTBE Obr-3609 (e.g., Holmes and Sues, 2000: figures 7, 8; Konishi *et* *al.*, 2012: figure 2; Makádi *et al.*, 2012: figure 4; Konishi *et al.*, 2015: figure 17L). These characteristics strongly suggest that the rib and the vertebra came from at least the middle, and more likely posterior, portion of the trunk.

Table 2 compares the character states of vertebrae available in the Obira specimen and selected basal mosasauroid taxa, and no taxon except the newly coded *Pannoniasaurus* demonstrates an exact match due partly to the missing data. *Aigialosaurus dalmaticus* and *Dallasaurus turneri* differ in having vertical condyles, and the latter also lacks a depressed condyle. Halisaurines generally lack zygosphenes and zygantra (e.g., Holmes and Sues, 2000: figures 7, 8), although incipient zygantra are reported on the posterior cervical vertebrae of *Phosphorosaurus ponpetelegans* (Konishi *et al.*, 2015: figure 17N). While much older stratigraphically, scores of *Aigialosaurus bucchichi*, *Komensaurus carrolli*, and *Haasiasaurus gittelmani* are consistent with those of the Obira specimen except for the missing data. One problem in the comparison of scores in such data matrices, however, is that vertebral morphology gradually varies within the column or even within the dorsal series, but these scores in data matrix represent only a particular segment(s) of the vertebral column available for observation. As well, at least in Mosasaurinae and Plioplatecarpinae, the number of zygapophyses along the dorsal series independently decreased phylogenetically (e.g. Lindgren *et al.*, 2008; Konishi and Caldwell, 2011; Cuthbertson and Holmes, 2015). The presence or absence state of articulation processes in vertebrae, including zygosphenes and zygantra, may therefore be not as phylogenetically informative and dependable.

It should be also noted that the vertebra of the Obira specimen is much larger than those of most basal mosasauroids, perhaps not so unexpected given its younger (= early Campanian) age. In most basal mosasauroid taxa including *Carsosaurus*, for which comparable detail of vertebral morphology is not available and not listed in Table 2, the dorsal centra are only up to a few centimeters long (Carroll and DeBraga, 1992; Caldwell *et al.*, 1995; Polcyn *et al.*, 1999; Bell and Polcyn, 2005; Caldwell and Palci, 2007). Meanwhile, the vertebrae referred to *Halisaurus* tend to be much larger: the dorsal centra of *H. arambourgi* are several centimeters long (Bardet *et al.*, 2005), whereas cervical centra of YPM 412, a specimen assigned to *H. platyspondylus*, measure up to 134.4 mm in length (Caldwell and Bell, 1995:542). With respect to other nominal halisaurine genera, well preserved cervical vertebrae of *Phosphorosaurus ponpetelegans* are approximately 50 mm long (Konishi *et al.*, 2015) and the dorsal vertebrae of *Eonatator sternbergii* (Wiman, 1920), often recognized as *Halisaurus* in a number of phylogenetic studies (e.g. Bell, 1997; Bell and Polcyn, 2005; Caldwell and Palci, 2007), are several centimeters long (TK pers. obs.). Finally, reported vertebrae of

Pannoniasaurus are several centimeters long on average but can be larger, based on the estimated maximum size of the animal at 6 m long (Makádi *et al.*, 2012). At present, the vertebra of Obr-3609 best compares in size with those larger vertebrae known to halisaurines, while morphologically it is most comparable to *Pannoniasaurus* vertebrae.

At this point, OTBE Obr-3609 cannot be identified to the genus level definitively, but the preserved morphological features indicate that it is a large basal mosasauroid for the reasons stated above. An early Campanian age of the Obira specimen predates that of *P. ponptetelegans* from the early Maastrichtian of Hobetsu, Hokkaido, indicating the presence of basal mosasauroids in the northwestern Pacific by at latest the early Campanian. Presence of well-developed zygantra in OTBE Obr-3609, a middle to posterior dorsal vertebra, is not known unequivocally in halisaurines so far, a feature that would align the Obira specimen better with *Pannoniasaurus* than with the former. At the same time, the anteroposteriorly elongate proportion characteristic of tethysaurine (*sensu* Palci *et al.*, 2013) vertebrae appears lacking in OTBE Obr-3609 (e.g., Makádi *et al.*, 2012: figure 6I).

Sato *et al.* (2012) noted a change in the numerical dominance of mosasaurines relative to russellosaurines from the Campanian in the Japanese mosasauroid fauna. The presence of halisaurines with mosasaurines in post-Santonian Cretaceous Period is also a well-documented global phenomenon (e.g., Bardet *et al.*, 2005; Konishi *et al.*, 2015: figure 21). Along with *Phosphorosaurus ponpetelegans* (Konishi *et al.*, 2015), if OTBE Obr-3609 indeed pertains to a halisaurine, the suggestion by Sato *et al.* (2012) that the Japanese mosasauroid fauna followed the global trends in terms of suprageneric taxonomic composition is further corroborated, although we cannot exclude a possibility at this point that Japan was also a home to a clade of large, presumably derived tethysaurines that survived into the early Campanian. Future discoveries of basal mosasauroid crania and pelvises in particular (e.g., Makádi *et al.*, 2012; Palci *et al.*, 2013) from the Campanian and older strata in Japan are expected to elucidate phylogenetic placement for specimens such as OTBE Obr-3609.

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Figure and table captions

Figure 1. Geology and stratigraphy of the mosasauroid specimen, OTBE Obr-3609. **A**. Index map of Hokkaido, northern Japan; **B**. Index map of the Cretaceous Yezo Group in Hokkaido, northern Japan; **C**, **D**. Locality of OTBE Obr-3609; **E**. Columnar section of upper part of Akano-sawa Creek.

Figure 2. Inoceramid bivalves from Akano-sawa Creek section. **A**. *Inoceramus* (*Platyceramus*) *japonicus* Nagao and Matsumoto, HMG-1813 from loc. 1; **B**. *Inoceramus* (*Platyceramus*) *ezoensis* Yokoyama, HMG-1680, from loc. 4; **C**. *Sphenoceramus naunanni* (Yokoyama), HMG-1681, from loc. 3.

Figure 3. Photographs of the dorsal vertebra of OTBE Obr-3609, Mosasauroidea gen. et sp. indet. **A**, anterior; **B**, ventral; **C**, posterior; **D**, left lateral; **E**, right lateral; and **F**, dorsal views.

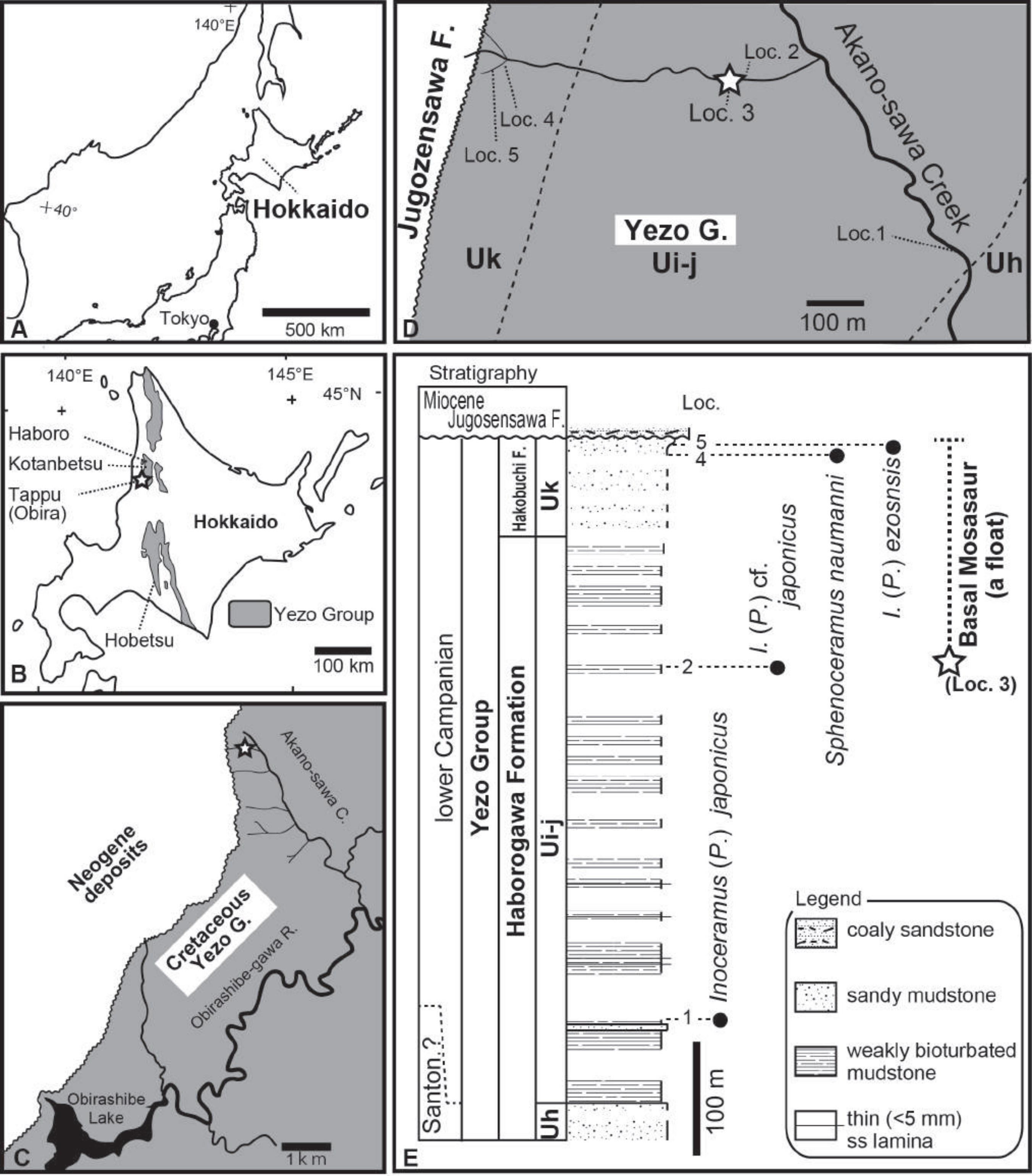
Figure 4. Interpretive drawings of the dorsal vertebra of OTBE Obr-3609, Mosasauroidea gen. et sp. indet. **A**, anterior; **B**, ventral; **C**, posterior; **D**, left lateral; **E**,

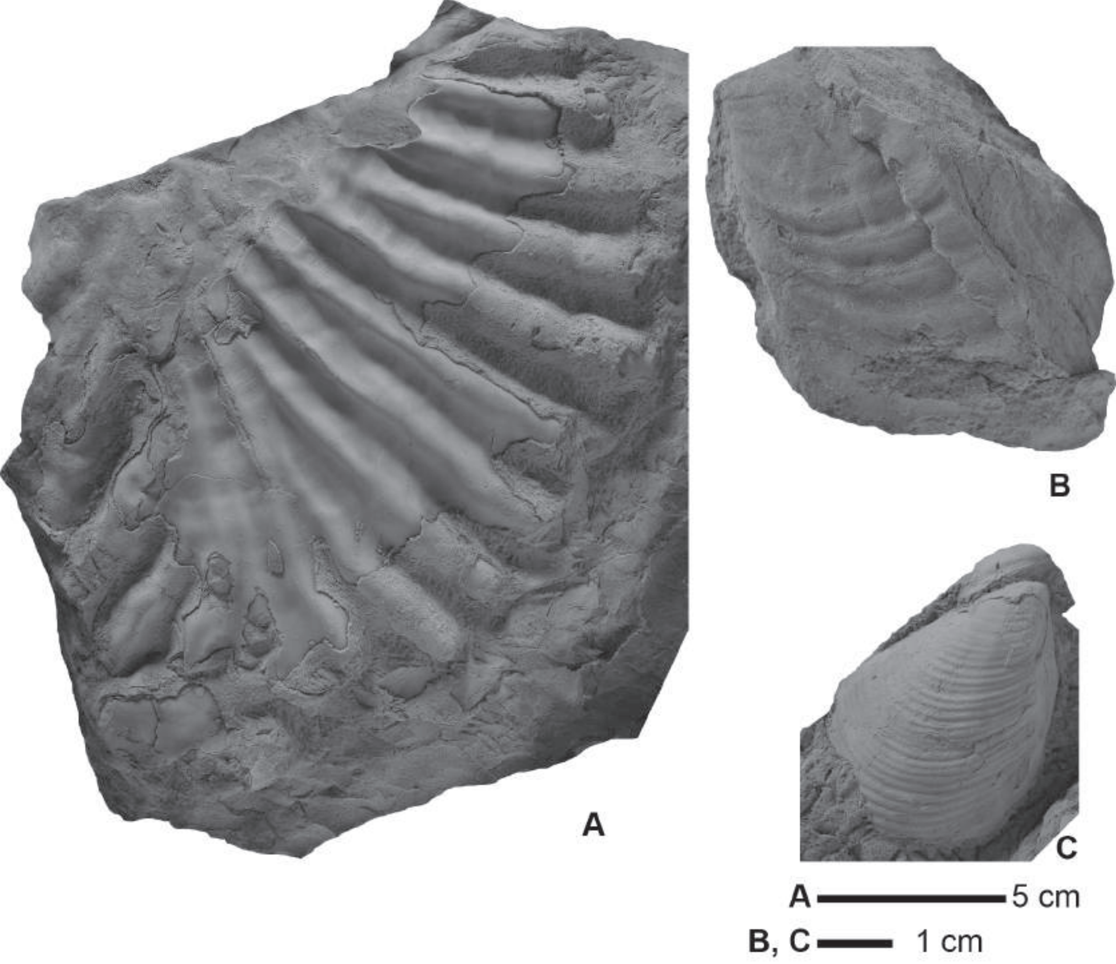
right lateral; and **F**, dorsal views. Abbreviations: cdl, condyle; ctl, cotyle; gr, groove; lr, lateral ridge; mr, medial ridge; poz, posterior zygapophysis; pozaf, articular facet of posterior zygapophysis; nc, neural canal; ns, neural spine (mostly broken); syp, symphysis; x, unnamed facet (see text); zt, zygantrum; ztaf, articular facet of zygantrum.

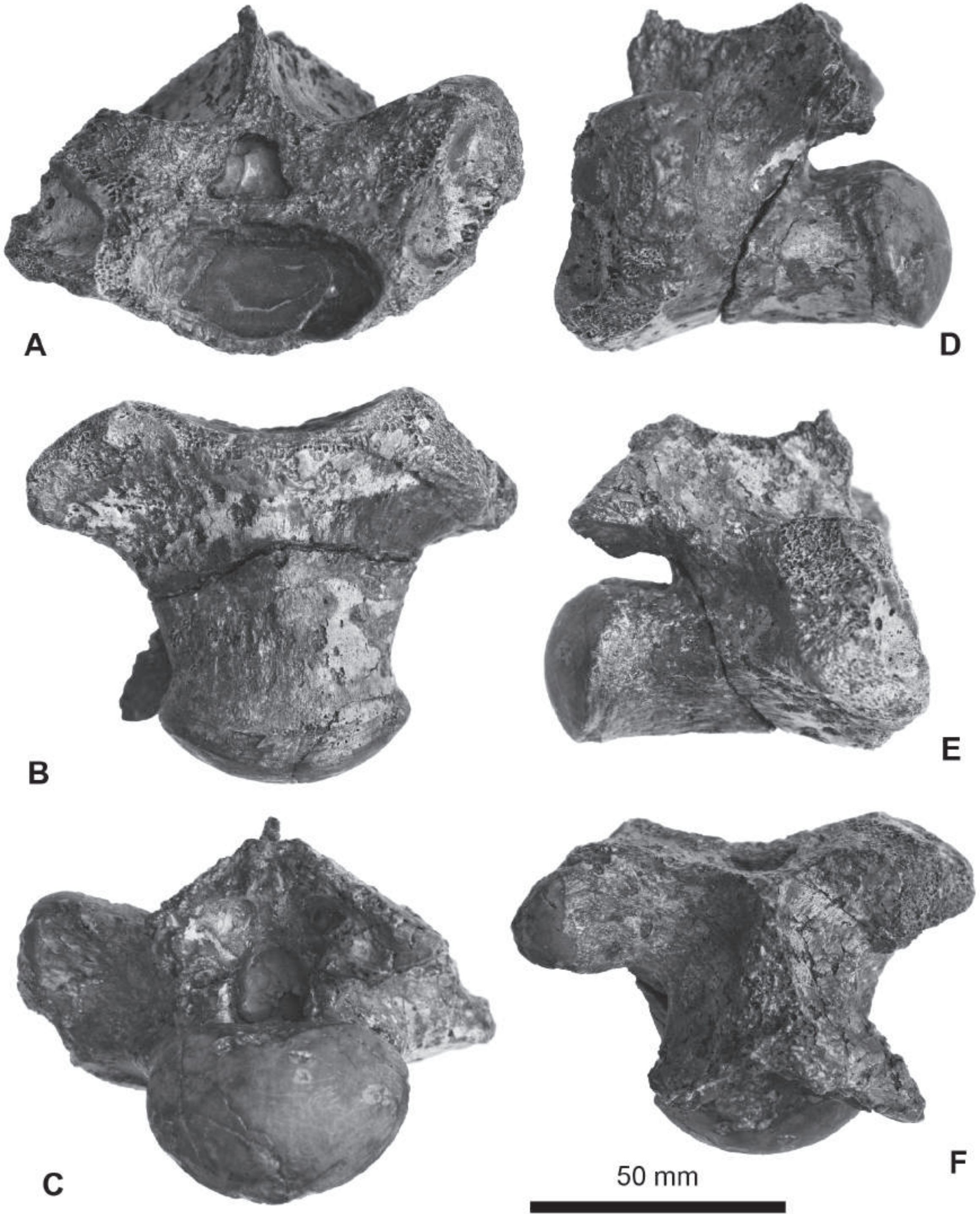
Figure 5. Photographs of the proximal rib fragment of OTBE Obr-3609, Mosasauroidea gen. et sp. indet. **A**, proximal, **B**, anterior; and **C**, dorsal views.

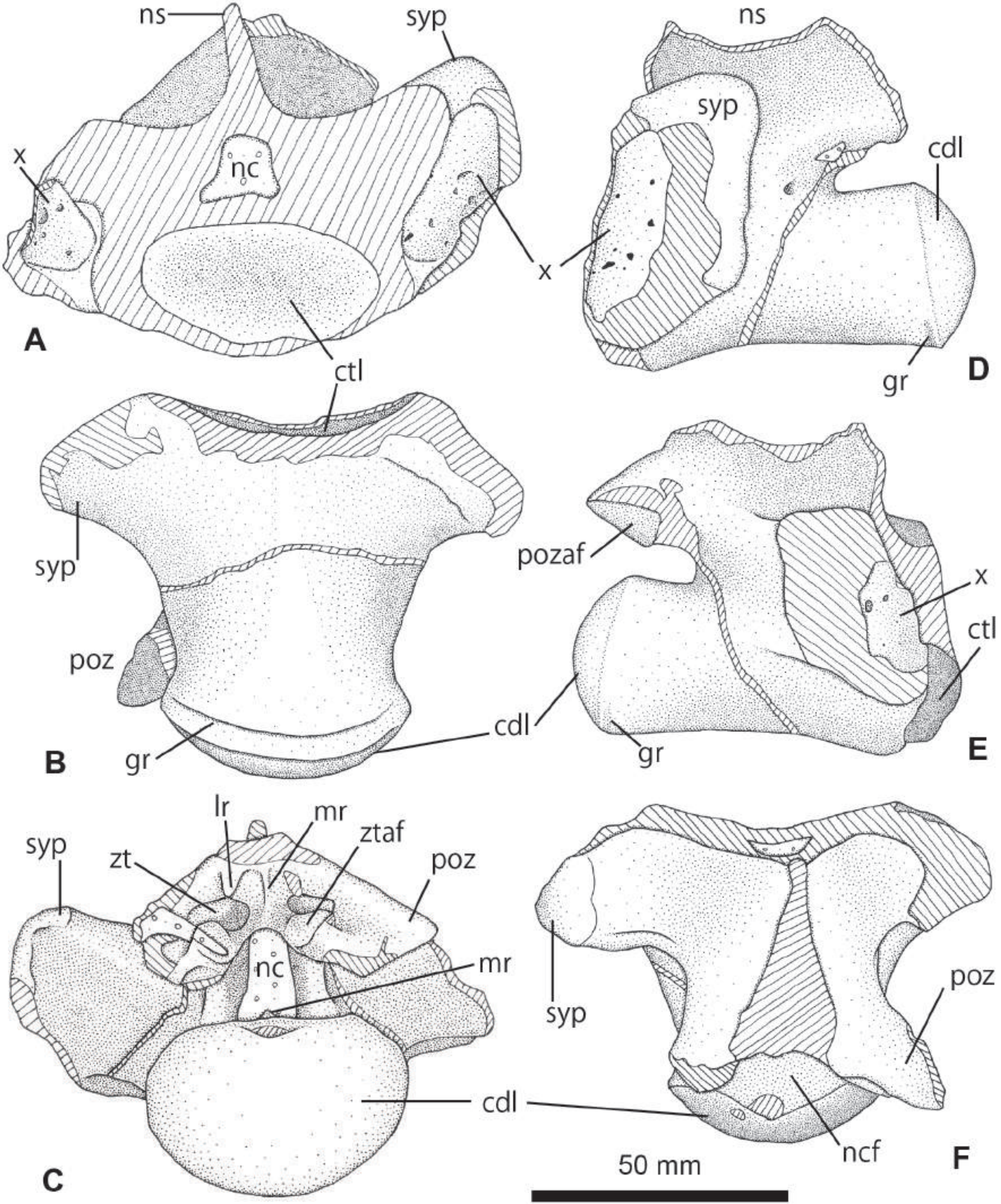
Table 1. Vertebral measurements (in mm) of OTBE Obr-3609, Mosasauroidea gen. et sp. indet.

Table 2. Comparison of vertebral characters in OTBE Obr-3609 and basal mosasauroid taxa. Scores for the characters from Dutchak and Caldwell (2009) were taken from their data matrix. Scores of *Komensaurus*, *Dallasaurus*, and *Haasiasaurus* for the Bell's (1997) character based on Caldwell and Palci (2007), Bell and Polcyn (2005), and Polcyn *et al.* (1999), respectively.


A
140°E
40°
Hokkaido
Tokyo
500 km
B
140°E
145°E
45°N
Haboro
Kotanbetsu
Tappu
(Obira)
Hokkaido
Yezo Group
Hobetsu
100 km
C
Akano-sawa C.
Neogene deposits
Cretaceous Yezo G.
Obirashibe-gawa R.
Obirashibe Lake
1 km
D
Jugozensawa F.
Loc. 2
Loc. 3
Loc. 4
Loc. 5
Akano-sawa Creek
Yezo G.
Ui-j
Uk
Loc.1
Uh
100 m
E
Stratigraphy
Miocene
Jugosensawa F.
lower Campanian
Santon.?
Yezo Group
Haborogawa Formation
Hakobuchi F.
Uk
Ui-j
Uh
Loc.
5
4
2
1
Inoceramus (P.) japonicus
I. (P.) cf. japonicus
Sphenoceramus naumanni
I. (P.) ezosnsis
Basal Mosasaur (a float)
(Loc. 3)
100 m
Legend
coaly sandstone
sandy mudstone
weakly bioturbated mudstone
thin (<5 mm) ss lamina


A
B
C
A 5 cm
B, C 1 cm


A
D
B
E
C
F
50 mm


ns
syp
x
nc
x
A
ctl
ns
syp
cdl
x
D
gr
ctl
syp
poz
gr
cdl
B
pozaf
x
ctl
cdl
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poz
ncf
F
50 mm

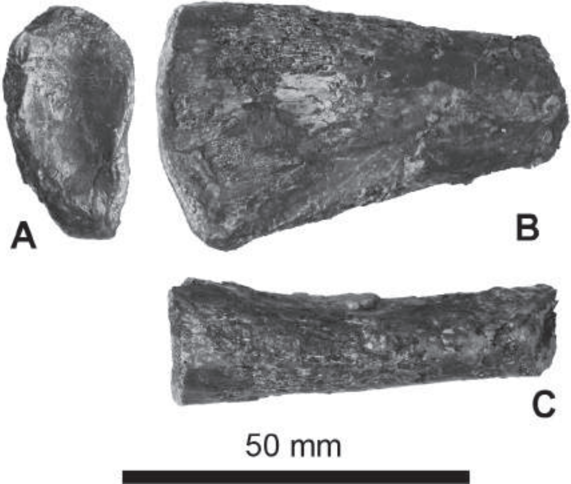
A
B
C
50 mm

Table 1. Vertebral measurements (in mm) of OTBE Obr-3609, Mosasauroidea gen. et sp. indet.

dimension	mm
centrum length along the ventral midline excluding condyle	67 (estimated)
center of condyle to the level of lateral edge of anterior intervertebral process	80 (estimated)
condyle width	52.4
condyle height	36.0

Table 2. Comparison of vertebral characters in OTBE Obr-3609 and basal mosasauroid taxa. Scores for the characters from Dutchak and Caldwell (2009) were taken from their data matrix. Scores of *Komensaurus* , *Dallasaurus* , and *Haasiasaurus* for the Bell's (1997) character based on Caldwell and Palci (2007), Bell and Polcyn (2005), and Polcyn et al. (1999), respectively.

Character source	character description	**OTBE-obr3609**	*Aigialosaurus bucchichi*	*Aigialosaurus dalmaticus*
Bell (1997, character 99)	zygapophysis present far posteriorly on trunk vertebrae (0), confined to anterior series (1)	**0**	0	0
Dutchak and Caldwell (2009, characters 80, 83, 85, 87)	Zygosphenes and zygantra: absent (0), or present (1).	**1**	1	1
	Synapophysis of middle trunk vertebrae not laterally elongate (0), or distinctly laterally elongate (1).	**0**	0	0
	Condyles of trunk vertebrae inclined (0), or condyles vertical (1).	**0**	?	1
	Condyles of posterior trunk vertebrae not higher than wide (0), or slightly laterally compressed (1).	**0**	?	?
This study	Precondylar constriction in precaudal vertebrae present (0), or absent (1).	**0**	1	?

Komensaurus	*Dallasaurus*	*Haasiasaurus*	*Halisaurus*	*Pannoniasaurus inexpectatus*
?	0	?	0/?	0
1	1	1	0	1
0	0	0	0	0
0	1	0	1	0
?	1	0	0	0
1	1	?	1	0