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A PARTIAL SKELETON OF TITANOSAURIAN SAUROPOD FROM THE EARLY CRETACEOUS OF TOBA CITY, CENTRAL JAPAN

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Abstract: A partial skeleton of a sauropod dinosaur was excavated from the Lower Cretaceous Matsuo Group (Valanginian to Barremian) in Toba City, central Japan. It preserves four caudal vertebrae, right and left humeri, and right and left femora. Other recovered bones are tentatively identified as left radius, right tibia, right fibula, and left ischium because of their fragmental preservation. This dinosaur is identified as a member of Titanosauria because it represents synapomorphies of the clade: (1) femoral fourth trochanter located on the caudomedial margin of the shaft, (2) approximately 0.89 of the humerus/femur length ratio, (3) presence of prominent "bulge" on the proximal lateral surface of the femur, (4) neural arch of middle caudal vertebra situated on the cranial half of the centrum, and (5) extreme eccentricity of the femur cross section (= 2.3). The combination of other characters may suggest that this dinosaur is a new taxon. The discovery of a possibly new titanosaurian dinosaur from the Early Cretaceous of Japan indicates that titanosaurians were more diverse in Asia, and their evolution was more complicated than previously thought.

Key words: Titanosauria, Early Cretaceous, Toba, Japan

INTRODUCTION

A large fragment of fossil bone was found by a group of armature fossil hunters on the seashore at Arashima-cho, Toba City, Mie Prefecture in July 1996 (Fig. 1). It was almost certain that the fossil was part of a large bone of a dinosaur because of the size and the geologic age (Early Cretaceous) of the fossil bearing formation. The discovery was soon reported to the Education Board of Mie Prefecture, and the Board organized the Dinosaur Research Group of Mie Prefecture, which conducted the following excavation and research.

Excavation was carried out for about two weeks in September 1996 (Fig. 2), and next three and half years were spent for cleaning and preparation of the specimens. The fossil bones were very poorly preserved, fossil bearing sediments were extremely hard, and many tiny faults and cracks also developed.

During the course of preparation, twelve bones were prepared and identified: four partial caudal vertebrae, right and left humeri, right and left femora, and fragments of possible left radius, right tibia, right fibula, and left ischium (Fig. 3). Because all the bones were found from more or less the same horizon and were distributed close together (less than ten meters in distance), and also there is no duplication of the same bones, it is assumed that they represent a partial skeleton of a single individual of dinosaur. It was nicknamed as "Toba dinosaur" after the city name where the fossil was found (Tomida *et al*., 2001)

Dinosaur Research Group of Mie Prefecture published a research report on this dinosaur in 2001, but it was written only in Japanese and some bones were later further prepared. Thus, this paper presents re-examination and re-description of those bones in English as well as discussion on the phylogenetic relationships based on more recent literature.

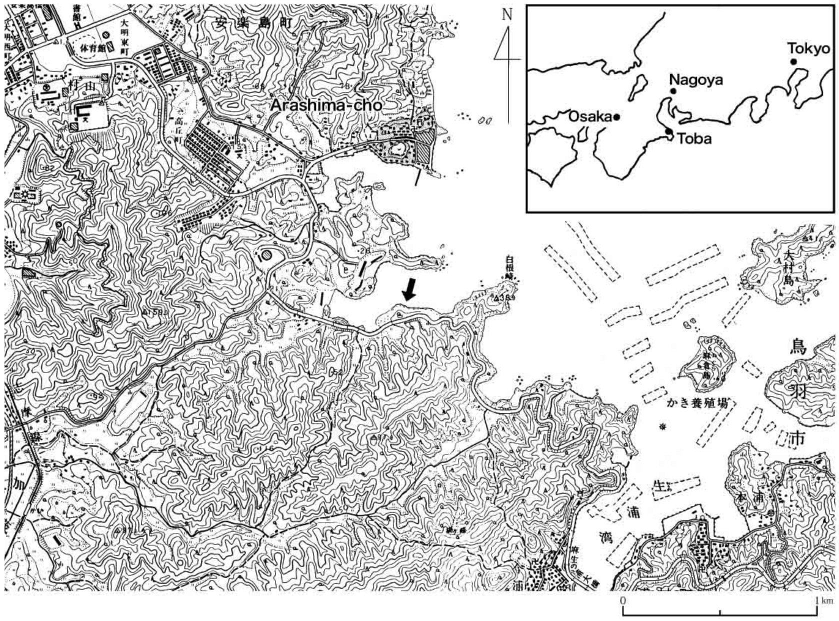

Fig. 1. Map showing the dinosaur fossil locality (arrow) at Tohama, Arashima-cho, Toba City, Mie Prefecture, Japan (after 1/25,000 topographic maps of Uramura and Toba, Geographical Survey Institute, Japan).

Fig. 2. Excavation and exposed fossil. Left, photo of excavation in September 1996; right, cross section of right humerus exposed on the rock surface (arrow).

GEOLOGY AND AGE

The area surrounding the fossil locality is one of the geo-tectonically most complex areas in Japan, and major geologic units are bounded by major faults including the Median, Mikabu, and Butsuzo tectonic lines (Saka, 2001a). The dinosaur fossil bearing beds are classified as Kamo belt of Matsuo Group, the latter of which is a unit of the Chichibu belt between Mikabu and Butsuzo tectonic lines. The Matsuo Group consists mainly of sandstones, mudstones, and alternation of those, and includes some conglomerates and rarely acidic tuffs. They include many brackish to shallow marine molluscs and sometimes trace and plant fossils. The Kamo belt of Matsuo Group near the dinosaur locality consists mainly of al-

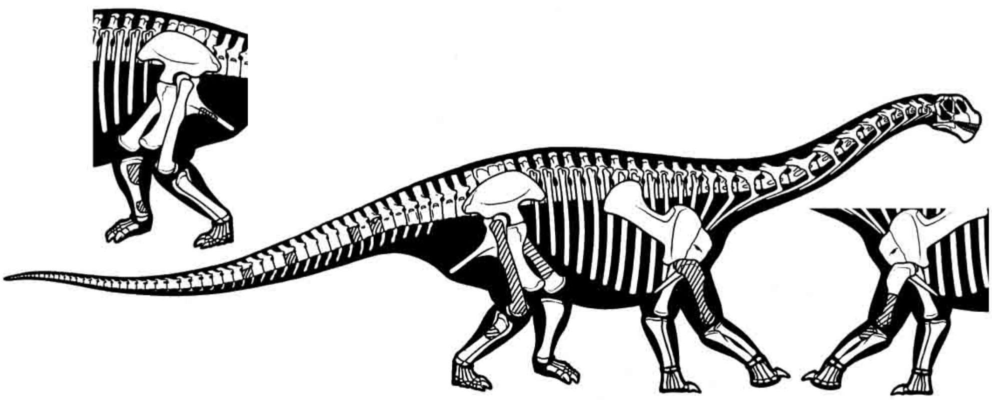

Fig. 3. Positions of preserved bones of Toba dinosaur (slash-marked area). Skeleton is of that of *Camarasaurus* after Wilson and Sereno (1998).

ternation of sandstones and mudstones with the thickness of a few to several tens of centimeters, and they often include concentrated beds of oyster and other bivalves, scattered bivalves (jointed or separated), and gastropods. The beds near the dinosaur locality have nearly east-west strike and steep south dip. They are dipping sometimes nearly 70 degrees to vertical (Saka, 2001a).

Toba dinosaur was found from black siltstone with about 50 cm thick within the Kamo belt. Two footprints of *Iguanodon*-like dinosaur were found on the exposure about 15 meters west of the Toba dinosaur quarry in 1998. Although it is difficult to measure the accurate stratigraphic position of the footprints against the horizon of the dinosaur because there are many small faults around there, they are probably about the same stratigraphic horizon. One of them is 50 cm long and 44 cm wide, while the other one is cut by micro fault (Fig. 8 of Saka, 2001a).

Yamagiwa (1957) suggested the geologic age of the Matsuo Group as the Early Cretaceous based on the molluscan fossils. Honda (2001) collected molluscan fossils near the Toba dinosaur locality and found that the fauna belongs to the Shiroi type molluscan fauna of Matsukawa (1979), which is supposed to be the Upper Berriasian to Hauterivian in age. Sugiyama *et al*. (1993) suggested the geologic age of the Matsuo Group as the Late Valanginian to Barremian based on radiolarian fossils collected from a locality about 500 meters southeast of the Toba dinosaur locality, while Kawabata (2001) indicates the age of Valanginian to Barremian based on the radiolarian fossils collected near the dinosaur locality. Saka (2001b) reports the fission-track age of the tuff bed just below theToba dinosaur horizon based on the zircon crystal as 138±7 Ma and the estimated age of the tuff as 130 Ma, which is the age of Hauterivian/Barremian boundary in most recent geologic time scale (Ogg *et al*., 2004).

DESCRIPTION

Toba dinosaur (Mie Prefectural Museum Fo-0014) is represented so far by four partial caudal vertebrae, right and left humeri, right and left femora, and fragments of possible left radius, right tibia, right fibula, and left ischium (Fig. 3). There are some other fragmentary bones, but none of them is identifiable their positions of the skeleton because of their fragmentary nature. Descriptions of each bone follow.

CAUDAL VERTEBRAE

Four caudal vertebrae are identified so far. They are all incomplete and are heavily deformed and broken, but they retain some morphological characters that help to identify their approximate positions within the caudal vertebrae and to help in identifying phylogenetic relationships. These four caudal vertebrae are here temporarily named as caudal vertebrae A to D, from anterior to posterior.

Caudal vertebrae of the sauropods are segmented into three regions based on the grade of development and presence or absence of neural spine, caudal rib, and haemal arch: proximal, medial, and distal. However, their definitions are not very strict, and there are some differences among them because of the individual variations of fossils and researchers. But, even so, they are approximately defined as follows (Upchurch pers. com., 2000; Barrett pers. com., 2000).

1) Proximal caudals: They possess caudal ribs and articular surfaces with haemal arches. In general, centrum is short anteroposteriorly and high dorsoventrally, and the first 14 to 16 caudals are classified in this category in majority of sauropod taxa.
2) Middle caudals: These do not possess caudal ribs but possess articular surfaces with haemal arches. Centrum is long anteroposteriorly and low dorsoventrally in comparison with the proximal caudals.
3) Distal caudals: These do not possess caudal ribs or articular surfaces with haemal arches. Centrum is much longer than height. In case of having neural spine, its posterior part is almost horizontal, or they do not possess the neural spine.

Caudal Vertebra A (Fig. 4 a-d; Table 1)

The centrum is relatively well preserved except that the right anterior and right posterior edges are missing, but it is rather strongly deformed. Also, it is cut by a micro fault running obliquely from central part of anterior surface to left lateral surface. Neural arch surrounding the neural canal is preserved, but the neural spine is missing. The centrum is weakly amphicoelus; anterior articular surface is moderately concave while posterior articular surface is weakly concave. Transverse cross section of the centrum is elliptical wider than height in outline. Ventral surface of the centrum is mildly excavated; this depression is formed by mediolaterally weak and anteroposteriorly strong curvature. This excavation is bounded by strong ventrolateral ridge on each side; the left one is much stronger than the right one, but it is thought to be deformed by lateral compression. There is another weak ridge above this strong ridge at the posterior half of the centrum; and at the anterior end of this weak ridge, there is a small hole with the size of 1 centimeter (cm) in length and 5 millimeters (mm) in height. It is difficult to say whether this hole is a remnant of pleurocoel. It is not possible to examine the presence or absence of the same ridge on the right side because of the breakage. Ratio of centrum length to height is about 1.5.

There is a small articular-facet-like surface at the area where the strong ventrolateral ridge meets the posterior articular surface, and it is probably the articular surface with a haemal arch. Among the neural arch, the only part surrounding the neural canal is preserved, and it is compressed from dorsolaterally and is deformed obliquely. Diameter of the neural canal is about 4 cm. Dorsal surface of neural arch forms a rather flat surface, and it is thought to be a “cut surface” by a fault or joint. Although the anterior most part is broken, the neural arch is located much anteriorly. The caudal rib is located in quite high position

Table 1. Measurements of caudal vertebrae (in mm).

Caudal vertebrae	A	B	C	D
Mediolateral diameter of anterior surface of centrum		155*		
Dorsoventral diameter of anterior surface of centrum		130*		
Mediolateral diameter of posterior surface of centrum	160*		120*	80*
Dorsoventral diameter of posterior surface of centrum	120*		80*	70*
Length of centrum	180*	150+	125+	

* estimated value; + over

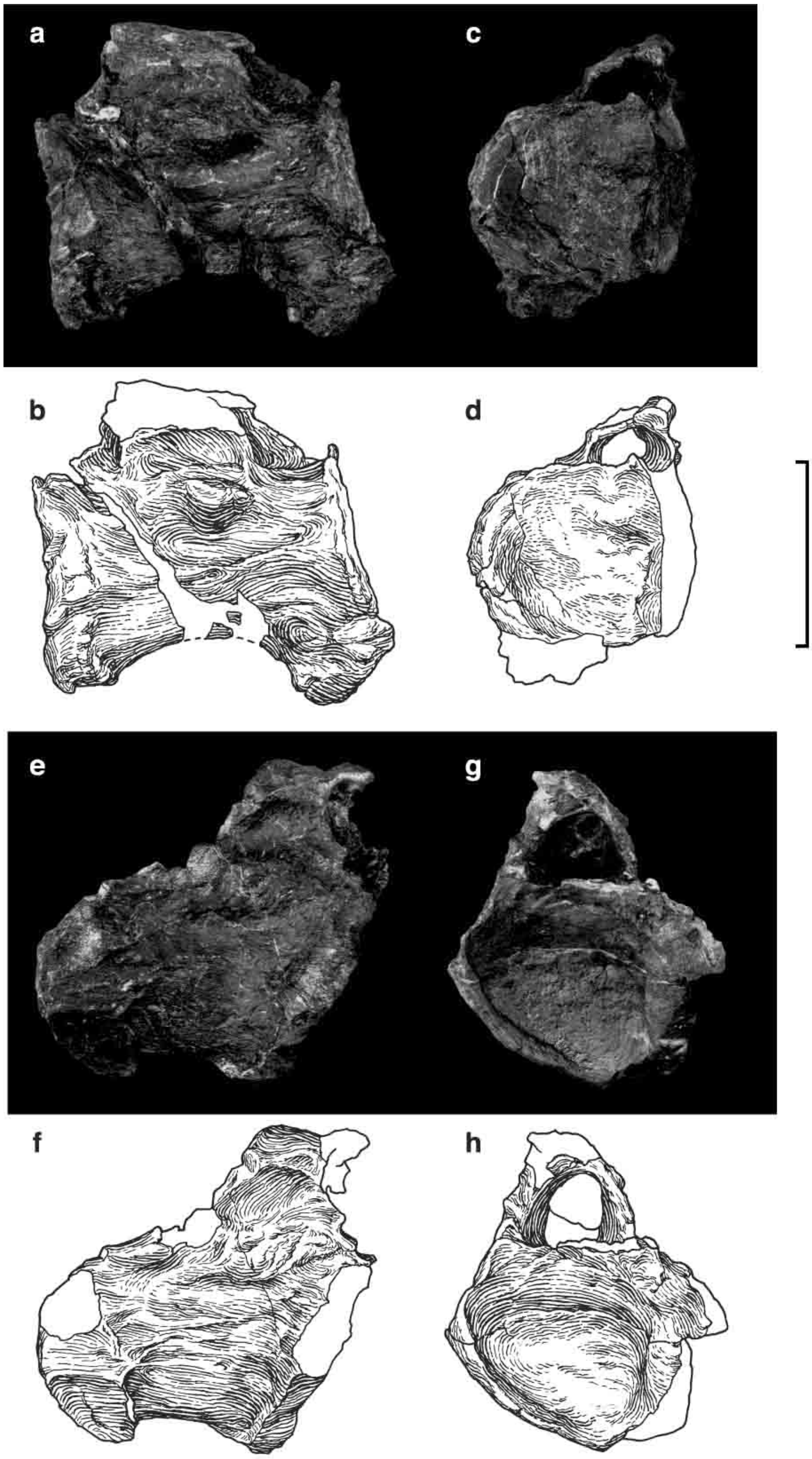

Fig. 4. Caudal vertebrae A and B. a-d: caudal vertebra A; e-h: caudal vertebra B; a, b: left lateral; c, d: posterior; e, f: right lateral; g, h: anterior views. Scale 10 cm (x 0.25).

and extends posterolaterally from the position that neural arch and centrum meet. Although the very tip is missing, it expands about 3 cm laterally and 6 cm anteroposteriorly, and it gets narrow toward the tip. Dorsal surface of the centrum posterior to the posterior end of neural arch forms a rather flat surface.

Based on the definitions above, it is clear that the caudal vertebra A of Toba dinosaur is one of the posterior proximal caudals. Comparing with those of *Apatosaurus ajax* of the National Science Museum (NSM-PV 20375; Upchurch *et al*., 2004), it may correspond 8th or 9th proximal caudal. Based on the illustrations of *Apatosaurus louisae* and *Opisthocoelicaudia skarzynskii*, caudal vertebra A is similar to 13th of *Apatosaurus louisae* and 9th to 10th of *Opisthocoelicaudia skarzynskii* (Gilmore, 1936; Borsuk-Bialynicka, 1977).

Caudal Vertebra B (Fig. 4 e-h; Table 1)

Posterior end of the centrum is missing, and posterior halves of left lateral and ventral portions are also missing with sharp cutting surfaces caused probably by a fault or joint. In addition, left half is deformed as if it was compressed posteriorly by strong pressure. Therefore, the centrum can be observed its morphology on the anterior, right lateral, part of left lateral, and dorsal surfaces. Part of the neural arch surrounding the neural canal is preserved, but neural spine is missing.

The anterior articular surface of the centrum is moderately concave as in the caudal vertebra A described above, and its edge is distinct and is rimmed by swell of about 1.5 cm wide. Transverse cross section of the centrum is elliptical wider than height. Ventral surface forms a shallow depression which curves weakly laterally and strongly anteroposteriorly, as in caudal vertebra A. This depression is bounded by a sharp ventrolateral ridge on right side, and there is articular-facet-like surface at the area where the ventrolateral ridge meets the swell on the rim of the anterior articular surface, and it is probably the articular surface with a haemal arch. There is a weak ridge, running anteroposteriorly, in the middle of right lateral surface of the centrum. The ratio of the length/height of the centrum is over 1.5 at least.

There is a swollen area on both side near the place where neural arch meets centrum, and they probably represent remnant of caudal ribs. Neural arch is situated at anterior half of the centrum. Neural canal is about 4.5 cm in diameter.

Because of the presence of remnant of caudal rib, caudal vertebra B is a proximal caudal, more posterior one than caudal vertebra A. It may correspond 10th to 11th of *Apatosaurus ajax* (NSM-PV 20375; Upchurch *et al*., 2004), 14th to 15th of *Apatosaurus louisae* (Gilmore, 1936), and 11th to 12th of *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977).

Caudal Vertebra C (Fig. 5 a-d; Table 1)

Caudal vertebra C preserves only a centrum, split into two parts with more or less same size. Transverse cross section is elliptical, and assuming the direction of a long axis is mediolateral. There are ridges on lateral surface of the centrum. On one of two other surfaces (dorsal and ventral), some bone fragments, possibly parts of neural arch, are preserved between the two blocks. The posterior surface has a shallow concavity.

Transverse cross section of the centrum is elliptical strongly elongated laterally, but degree of lateral elongation probably be exaggerated by deformation caused by compression, in comparison with other caudal vertebrae. A strong ridge runs anteroposterioly on the middle part of right lateral surface, and a weak ridge is also present near the ventral edge, whereas the middle part of left lateral surface is rather flat and there are two weak ridges (dorsal one is somewhat stronger) that border the dorsal and ventral surfaces. The difference of morphology between left and right lateral surfaces is probably because of the deformation of right side.

A number of bone fragments in different size between two separated blocks of the centrum seem to be part of crashed neural arch. It is not possible to examine the caudal rib because of this breakage. Only sediments can be seen in the separated area between two blocks on ventral view. Anterior surface is broken, and a number of bone fragments are observed, but there is no remain of original articular surface.

Based on the morphology described above and the comparisons with caudal vertebrae A and B, caudal vertebra C is one of the middle caudals located at about 1/3 from the anterior end of whole middle caudals. Caudal vertebra C may correspond 18th to 19th of *Apatosaurus ajax* (NSM-PV 20375, Upchurch *et al*., 2004) and 17th to 18th of *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977).

Caudal Vertebra D (Fig. 5 e-h; Table 1)

This partial caudal vertebra was attached to caudal vertebra C when the research report was published in Japanese (Tomida *et al*., 2001), but it was later separated by preparation. Posterior half of the centrum and part of the lateral wall of neural canal in both sides are preserved.

Transverse cross section of the centrum is nearly square with rounded corners, and the ventral surface is nearly flat. There are articular facet like structures in both sides at the posterior end of ventral surface, and they are thought to be the articular surfaces with haemal arch. There are ridges on the both lateral surfaces, slightly above the midline. Posterior articular surface is slightly concave. Neural canal is esti-

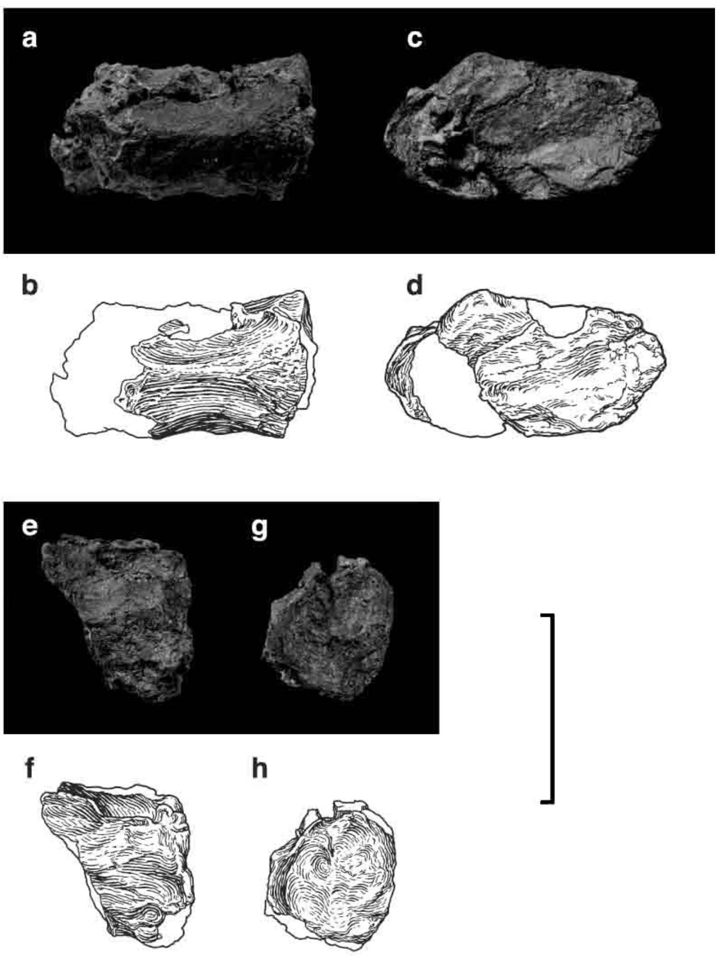

Fig. 5. Caudal vertebrae C and D. a-d: caudal vertebra C; e-h: caudal vertebra D; a, b: left lateral; c, d: posterior; e, f: left lateral; g, h: posterior views. Scale 10 cm (x 0.25).

mated about 1 cm in diameter.

Based on the morphology described above and the comparisons in size with other caudal vertebrae (table 1), caudal vertebra D is thought tobe one of the middle caudals that are located in the middle or slightly posterior within the whole middle caudals. It may correspond 22nd to 24th of *Apatosaurus ajax* (NSM-PV 20375, Upchurch *et al*., 2004) and 20th to 21st of *Opisthocoelicaudia skarzynskii* (Borsuk-Bialynicka, 1977).

HUMERI

Right Humerus (Fig. 6; Table 2)

Right humerus is the second largest bone among the Toba dinosaur skeleton, and the maximum length of the preserved portion is approximately 115 cm. Approximately lateral two-thirds ofproximal end is missing by a fault running posterodorsally to anteroventrally, and medial one-third of proximal end is missing by breakage before burial and during excavation. Thus, morphology of proximal end is unobservable. On the anterior surface of the distal end, the compact bone is preserved fairly well except for a part of anteromedial portion. Anterior part of rough surface of the proximal end is preserved at ap-

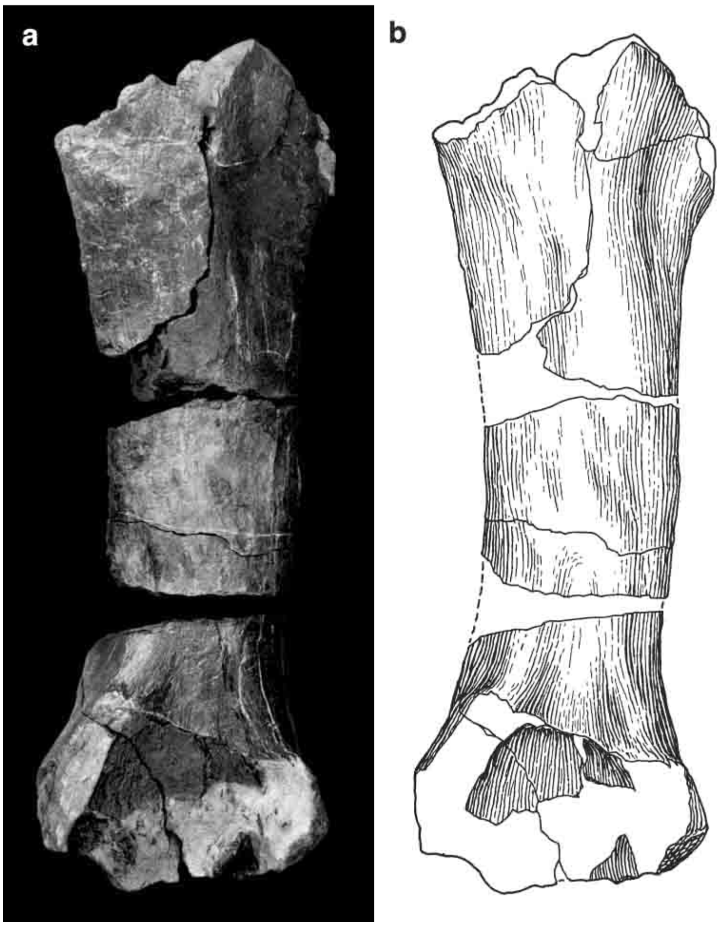

Fig. 6. Right humerus. a, b: posterior; c, d: anterior; e: medial views. Scale 50 cm (x 0.1).

proximately lateral two-thirds, and the border with compact bone of anterior face is swollen. The area of about 30 x 20 cm on the posterior surface of distal portion caved in, and there remain some platy fragments of compact bone. The cave-in occurred probably by stress of sediments after spongy bone became

Table 2. Measurement of humeri (in mm).

	Right	Left
Maximum length, estimated	1250	-
Maximum length, preserved	1150	580
Maximum width at proximal end	400	-
Maximum width at distal end	405	450
Mediolateral diameter at thinnest point (about 1/3 from distal end)	265	260
Anteroposterior diameter at thinnest point	120	120
Circumference at thinnest point	625	612

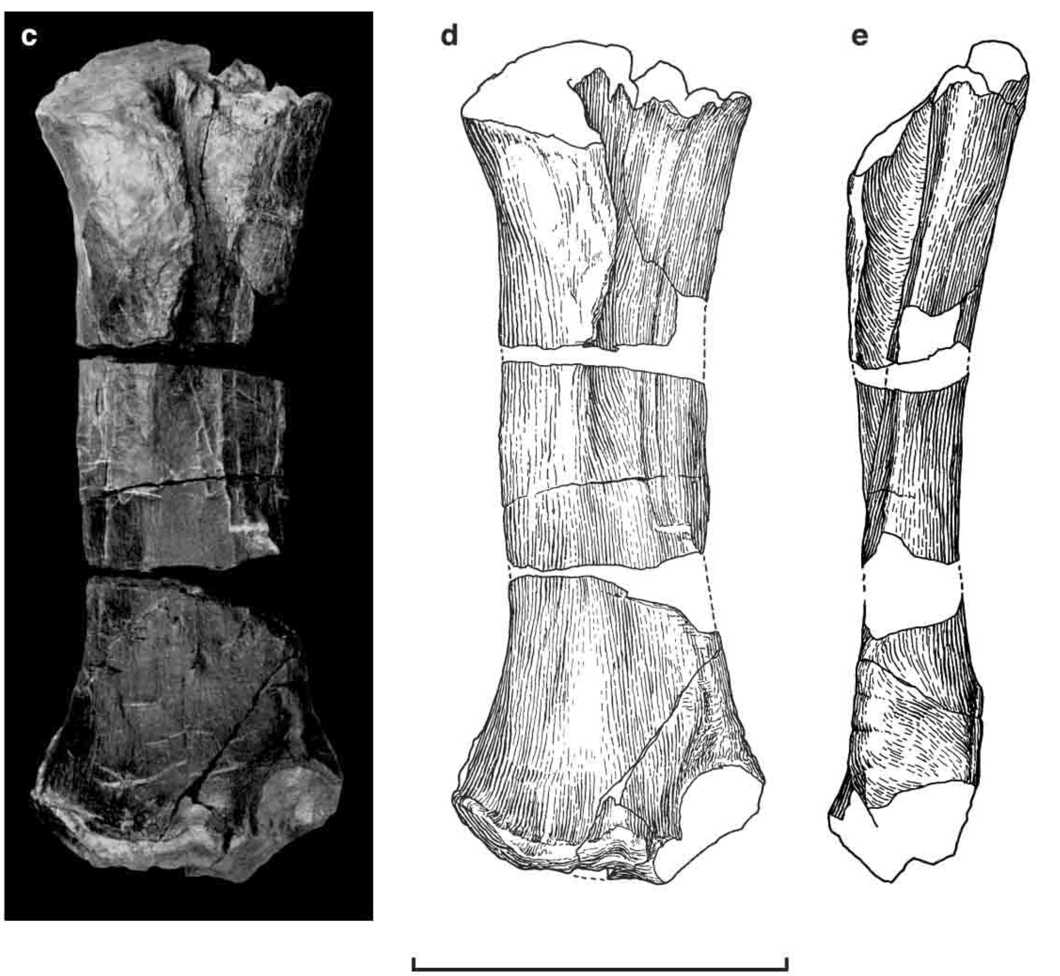

Fig. 6. *Continued.*

fragile with some kind of reason (e.g. weathering before burial?). The area originally spongy bone occupied is filled with the mixture of fragmentary spongy bones and mud, and it is extremely difficult to distinguish between bone and sediments.

Expansion of proximal and distal ends of the humerus in mediolateral direction is weak, while constriction of middle shaft is very weak, so that the general outline in posterior and anterior views is somewhat tree trunk like. It is common in other sauropods that medial portion of proximal one-third or one-half strongly expands medially, but it is very weak in this specimen. It is difficult to judge whether this is original morphology or not, but it may be possible that the humerus reduced its width by compression of mediolateral direction, because there are a few parallel cracks running proximal-distal direction, indicating to have received compression in mediolaterally. However, because these cracks extend to the middle part of the shaft, they may not explain the weakness of medial expansion of proximal portion.

In anterior view, deltopectoral crest develops strongly on the proximal one-third of the shaft and overhangs to the anterior surface of the shaft. In posterior view, somewhat wide ridge that reaches medial articular condyle develops along the mediodistal edge, but its higher portion is missing by joint-like fracture so that the height and morphology of the ridge is unknown. Horizontal cross section of the shaft at about one-third from the distal end is almost elliptical, with the anterior part flatter than the posterior.

Left Humerus (Fig. 7; Table 2)

Left humerus remains approximately distal one half. The distal end is missing by a small fault running obliquely anteroposteriorly, so that its shape is unknown. The area of 33 x 25 cm at maximum on the posterior surface of distal portion caved in, and there remain some platy fragments of compact bone. The largest fragment seems to fit the rest of the shaft, if it is moved upward for about 8 cm (Fig. 7 a, b). This cave-in is almost the same as the right humerus in its position, size, and condition. Although somewhat wide ridge that reaches medial articular condyle develops medio-distally, but it is heavily broken except its proximal end so that the height and shape of the ridge is unknown. This condition is also the same as the right humerus.

Maximum width near the distal end is 45 cm, which is about 10% wider than that of right humerus. It is unknown whether the difference is original or caused by the lateral stress of cave-in. There is not much characteristic feature on the anterior surface. Transverse cross section of the shaft at about 1/3 from the distal end (where the shaft is most slender) is almost identical with that of right humerus in outline and size.

FEMORA

Right Femur (Fig. 8; Table 3)

It is the largest bone among the Toba dinosaur skeleton, and the maximum length of preserved portion is 128 cm. It is broken into four major blocks, but it seems to keep the original morphology except for both proximal and distal ends. At the proximal area, a part of the proximal end of the shaft and the head are missing. In posterior view, distal portion is rather well preserved, but the distal end is unclear because it is difficult to distinguish between bone and sediments. In anterior view, the area near the lateral articular condyle caves in by pressure, while the area near the medial articular condyle is missing because ofa fault or joint running obliquely. The distal portion is not only heavily damaged but also the distinction between bone and sediments is difficult. Therefore, the preparation is not completed in this part, and the total length of the bone is estimated as about 140 cm.

This femur is slightly curved with the anterior surface convex. The sauropod femora are always straight, therefore this curvature must be a result of postmortem deformation. The shaft is extremely thin anteroposteriorly, and transverse cross section is long elliptical or wide subrectangular in outline. The ra-

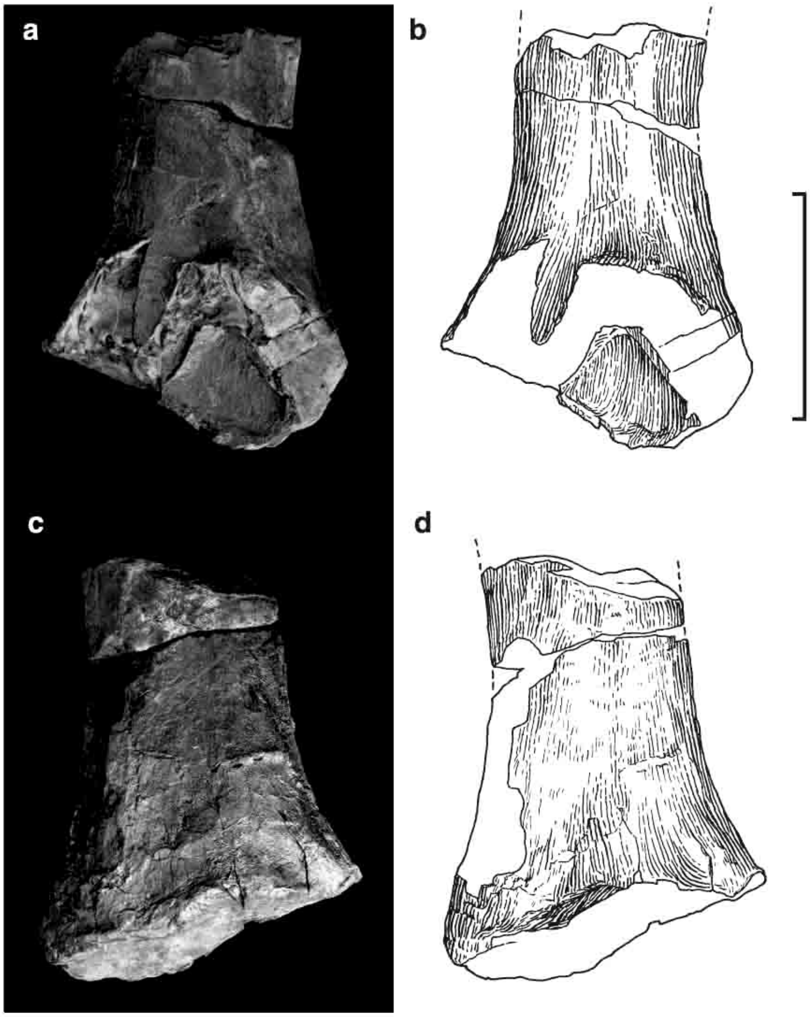

Fig. 7. Left humerus. a, b: posterior; c, d: anterior views. Scale 30 cm (x 0.1).

tio of lateral width to anteroposterior thickness (335/145 mm) is about 2.3, which is very large. The head is missing. The lateral "bulge" (Upchurch, 1998) is present on the lateral surface at about one-quater from proximal end. Lateral and medial condyles of distal end are about the same size as far as observable, but the specific size and shape is unknown because of the cave-in and breakage.

The fourth trochanter is present on the medial surface to posteromedial margin of the shaft at about one-third from the proximal end and is formed in an area of 25 cm long and 10 cm wide with rough surface.

Left Femur (Fig. 9; Table 3)

Left femur was found and excavated in 1998 (one and half years after the original excavation) from the same site. It is cut into four major blocks by micro faults, and calcite veins are formed between them, as well as thinly sliced bones are sandwiched in the calcites. Partial shaft of the femur approximately 75 cm in length in total, of which medial 2/3 of anterior surface and the medial surface, is preserved. Proximal end of the preserved portion is the proximal end of the fourth trochanter. Posterior surface is caved in, as

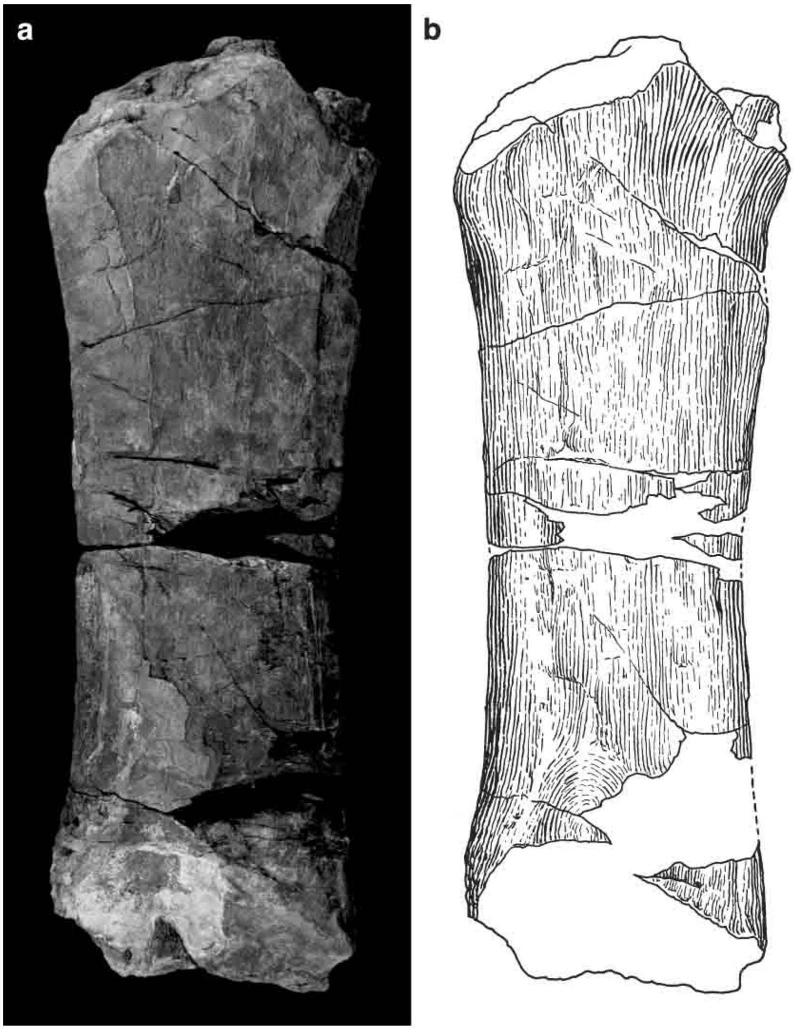

Fig. 8. Right femur. a, b: anterior; c, d: posterior; e: medial views. Scale 50 cm (x 0.1).

in the cases of distal portion of humeri, and fragments of compact bone remain there with the largest piece measures 20 cm in length and 4 cm in width (Fig. 9 c). Majority of spongy bone is lost.

The most characteristic feature is the rough surface of the fourth trochanter. It is located on the medial surface to posteromedial margin of the shaft near the proximal end of the preserved portion (Fig. 9 a, b), and it is recognized as an ellipical to subrectangular area of about 25 cm in length and 9 cm in maximum width with extremely bumpy surface. The medial surface just below the rough surface of the fourth trochanter is smooth and rounded. Further below that (the distal most block), the medial surface is almost flat and meets with anterior surface almost perpendicularly. This is probably deformation caused by stress. The rough surface of the fourth trochanter is not perpendicular to the anterior surface but rather facing somewhat anteriorly, but this is also probably the result of deformation.

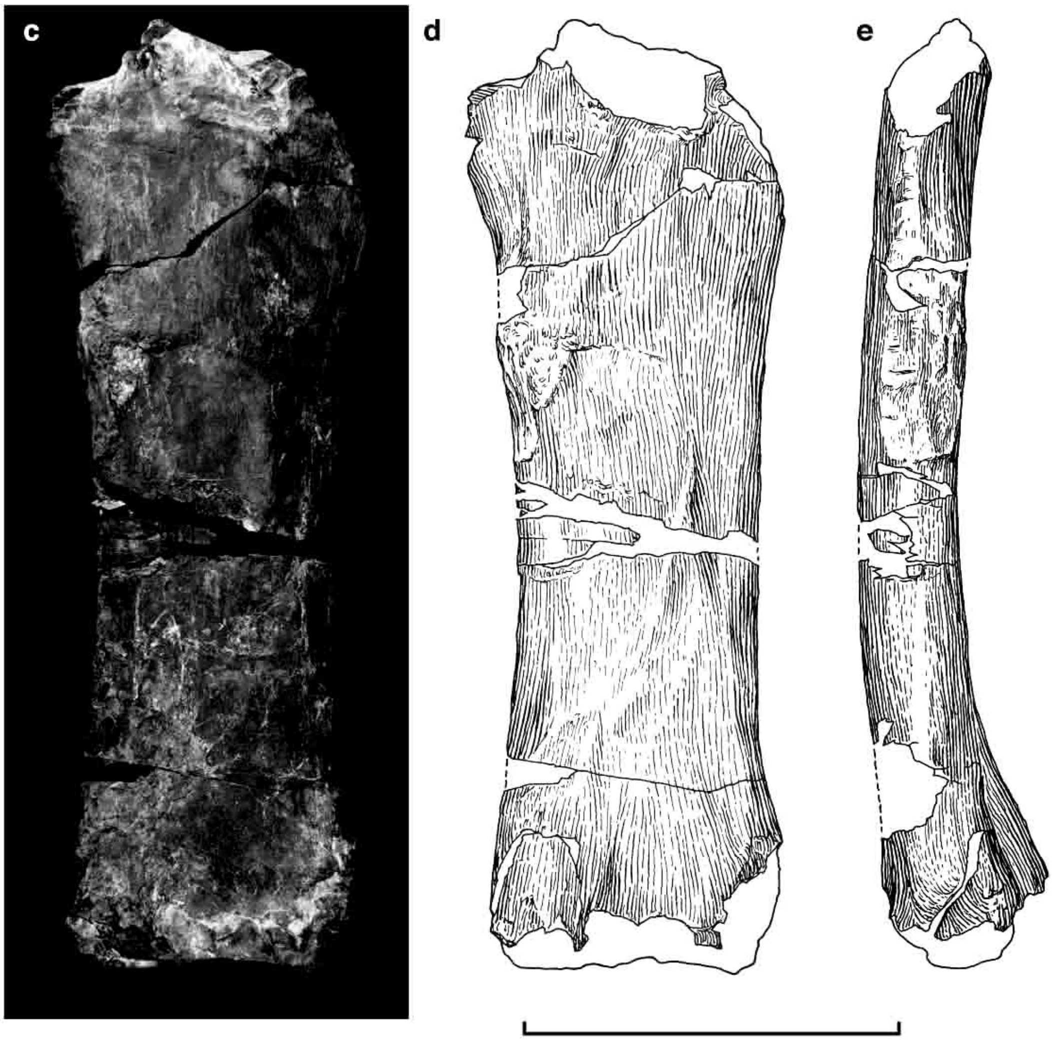

Fig. 8. *Continued.*

Table 3. Measurement of femora (in mm).

	Right	Left
Maximum length, estimated	1400	-
Maximum length, preserved	1280	ca. 750
Mediolateral diameter at thinnest point (ca. middle of shaft)	335	-
Anteroposterior diameter at thinnest point	145	-
Circumference at thinnest point	804	-
Maximum width at the point of lateral bulge	400	-

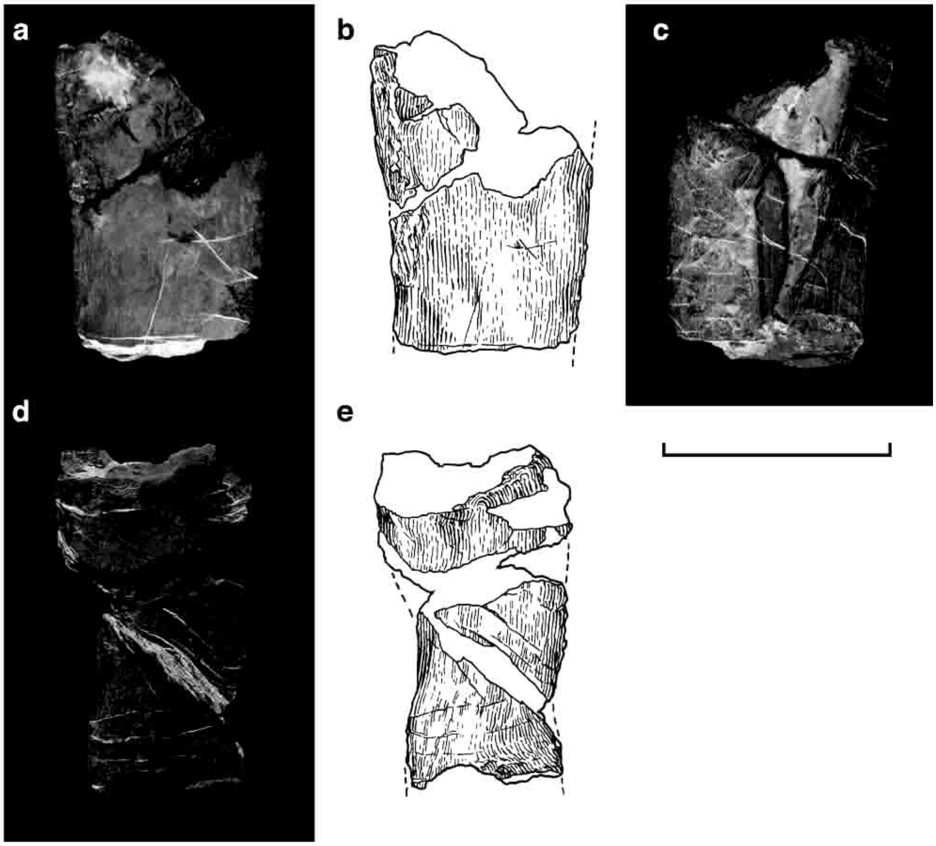

Fig. 9. Left femur. a, b: anterior views of proximal ca. 1/3; c: posterior view of proximal ca. 1/3; d, e: anterior views of middle shaft ca. 1/3. Scale 30 cm (x 0.1).

OTHER BONES

Left Radius (Fig. 10)

This bone is approximately proximal one-third of left radius, but the rough surface of the proximal end is not preserved. Proximal end is elliptical in outline, of which lateral portion is somewhat expanding laterally, while medial portion is almost parallel to the long axis of the ellipse. This lateral expansion is the part that articulates with ulna. From proximal toward distal direction, mediolateral diameter becomes smaller, while anteroposterior diameter becomes smaller for the first ca. 10 cm but then does not change. Horizontal cross section of the shaft is elliptical in outline, and it is about the same from proximal to distal. Proximal portion of anterior surface is rather flat, while distal portion of posterior surface becomes somewhat ridge like. Measurements are as follows: maximum length of preserved portion, 283 mm; maximum anteroposterior diameter of proximal end, 199 mm; maximum mediolateral diameter of proximal end, 158 mm; maximum anteroposterior diameter of distal end, 154 mm; maximum mediolateral diameter of distal end, 86 mm.

Right Tibia (Fig. 11 a, b)

A fragment of a large bone with subcircular horizontal cross section (about one-third of subcircular preserved) is identified as a fragment of proximal portion of right tibia, based mainly on the comparison

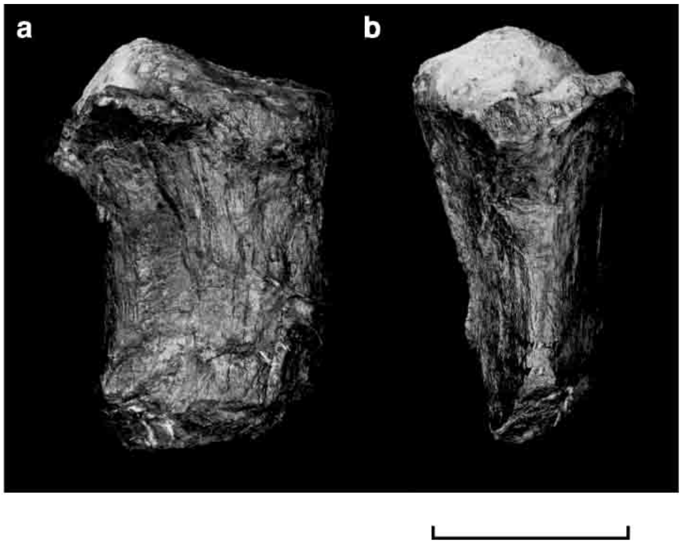

Fig. 10. Left radius. a, medial; b, posterior views of proximal portion. Scale 13 cm (x 0.2).

with the original skeleton of *Apatosaurus ajax* (NSM-PV 20375; Upchurch *et al.*, 2004). Figure 11a shows part of medial surface and part of posterior surface of the shaft. The projected area on the right upper corner of figure 11a is not part of tibia but unprepared rock and fragments of unidentified bone. Medial surface is rather flat and curves gently medially toward proximal end. On the cross section, it can be observed that compact bone changes to spongy bone, and further inside, spongy bone is missing and muddy matrix occupies the space. Maximum length and anteroposterior diameter of the preserved portion is 290 mm and ca. 200 mm, respectively.

Another fragmentary bone (Fig. 11 b) is tentatively identified as medial portion of distal shaft of right tibia, based mainly on the direct comparison with the skeleton of *Apatosaurus ajax* (NSM-PV 20375; Upchurch *et al.*, 2004). Medial surface curves strongly medially toward distal end, making the mediolateral diameter thicker. Maximum length and anteroposterior diameter in proximal end of preserved portion are 183 mm and 142 mm, respectively.

Right Fibula (Fig. 11 c)

This bone fragment is partial shaft of right fibula, representing approximately one-quarter to one-third from proximal end. Horizontal cross section is a narrow isosceles triangle with rounded corners in outline, of which the base side of triangle is posterior surface. Diameter becomes smaller, and the shaft curves slightly laterally, toward distal direction. Measurements are as follows: maximum length of preserved portion, 215 mm; anteroposterior and mediolateral diameters at proximal end, 142 mm, 100mm; and anteroposterior and mediolateral diameters at distal end, 119 mm, 75 mm.

Left Ischium (?) (Fig. 11 d)

A platy bone fragment of about 30 cm x 14 cm, with weak concave surface on one side and weak convex surface on the other, is tentatively identified as part of middle portion of left ischium, based mainly on the direct comparison with the original skeleton of *Apatosaurus ajax* (NSM-PV 20375; Upchurch *et al.*, 2004). Lateral surface is weakly concave and rather smooth, while medial surface is weakly convex and shows many cracks. These cracks may have caused by weathering before burial. Ventral edge be-

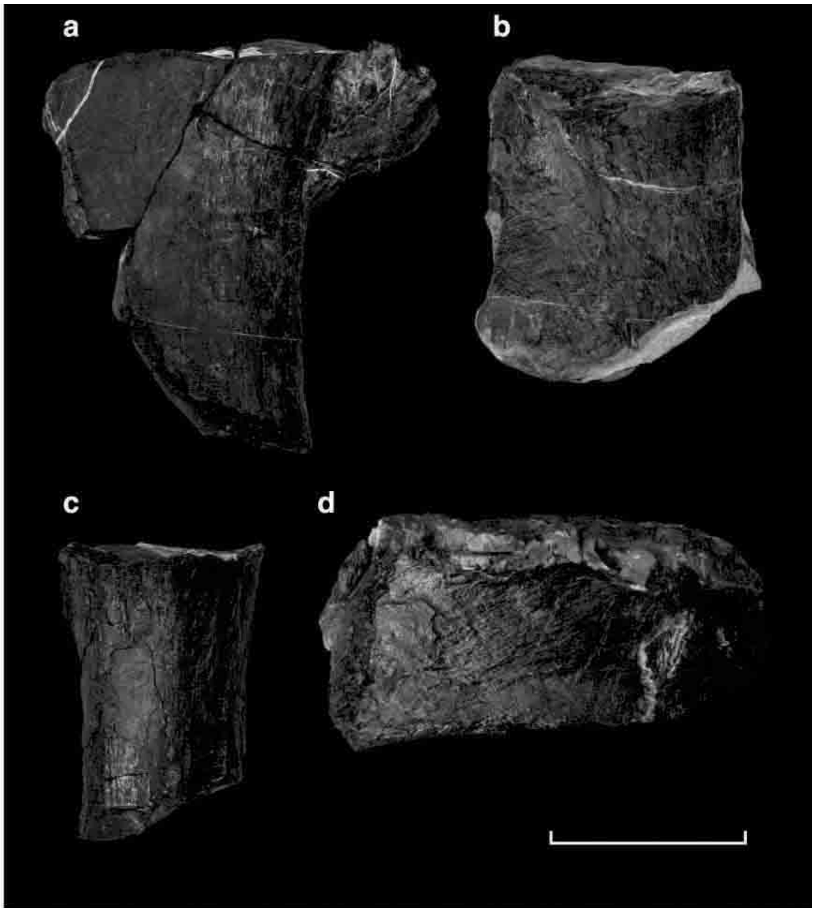

Fig. 11. Right tibia, right fibula, and possible left ischium. a, proximal portion of right tibia in medial view; b, distal portion of right tibia in medial view; c, middle to proximal portion of right fibula in posterolateral view; d, part of middle portion of possible left ischium in lateral view. Scale 13 cm (x 0.2)

comes thin and forms a ridge. Maximum anteroposterior length and dorsoventral width of preserved portion are 298 mm and 140 mm, respectively.

DISCUSSION

Studies on the evolutionary relationships among sauropods based on the cladistic analysis have rapidly been developing in recent years (e.g., Upchurch, 1995, 1999; Calvo and Salgado, 1995; Salgado *et al.*, 1997; Curry Rogers and Forster, 2001), and especially since 1998, several representative papers on phylogenetic relationships of Sauropoda have been published (Upchurch, 1998; Wilson and Sereno, 1998; Upchurch *et al.*, 2004). Upchurch *et al.* (2004) is the most recent and detailed (309 characters, and 41 genera) analysis. As described in the previous section, Toba dinosaur includes limited number of bones (Fig. 3), and informative characters for phylogenetic analysis can be obtained only from four caudal vertebrae, two humeri, and two femora. Because the number of characters obtained is very limited, we tried to test the phylogenetic position of Toba dinosaur by applying each character on the cladogram presented by Upchurch *et al*. (2004) (Fig. 12). However, they do not show the data sets and description of each character, but they mention that it is based mainly on "a synthesis of the data sets presented by Upchurch (1998, 1999) and Wilson and Sereno (1998)." Wilson and Sereno (1998) used 109 charachters and 10 taxa, and they combined Titanosauria as a single taxon; while Upchurch (1998) used 205 characters and 26 genera, and Titanosauroidea (comparable to Titanosauria of Wilson and Sereno, 1998 and of Upchurch *et al*., 2004) is analyzed in more detail. Although Upchurch *et al*. (2004) is more detailed, their result (Fig. 12) is rather similar to that of Upchurch (1998), especially the taxa higher than Camarasauromorpha.

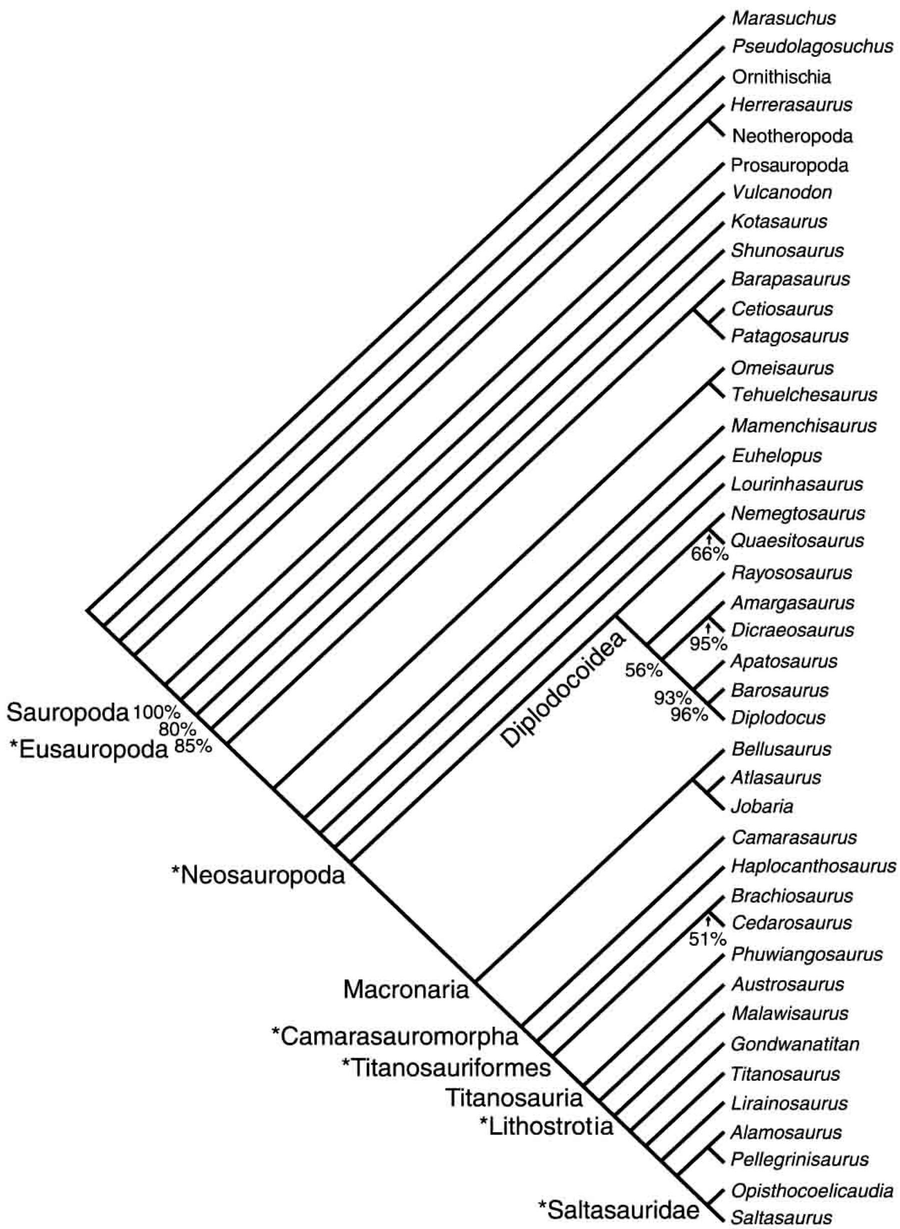

Fig. 12. Cladogram of 41 sauropod genera (after Upchurch *et al.*, 2004).

Therefore, discussion below is based mainly on the comparison with Upchurch (1998).

Among those 205 characters that Upchurch (1998) used, only fifteen characters can be observed (Appendix 1). Comparisons on the fifteen characters with *Brachiosaurus* and higher taxa based on the cladogram by Upchurch (1998, figure 19) are on Table 4. Based on Appendix 1 and Table 4, it is certain that phylogenetic position of Toba dinosaur is at node K of Upchurch (1998) (=Titanosauriformes in Fig. 12) or higher because the neural arches of middle caudals are positioned on the cranial half of the centrum and there is a prominent bulge on the lateral surface of the femur (Appendices 1 and 2). Although, among the synapomorphic characters from node A to K, only nine characters can be scored from the Toba dinosaur (from 138 through 191 in Table 4), there is no character inconsistent with the statement above.

Furthermore, the Toba dinosaur shows affinities with Titanosauria in Fig. 12 or Titanosauroidea of Upchurch (1998) based on the following two rationales. Primary, the horizontal cross section of femur being elliptical extremely wider mediolaterally is the character of Titanosauria of Wilson and Sereno (1998) (Wilson and Carrano, 1999), and Toba dinosaur has much larger value (2.3) than the value (1.85) Wilson and Carrano (1999) indicated. Secondly, in Table 4, the Toba dinosaur and *Brachiosaurus* have different character state for C132, C136, and C137, indicating that the Toba dinosaur may belong to the clade of Titanosauria.

Based on the character status of the Toba dinosaur (Table 4), the combination of character conditions from C129 to C137 is unique and may suggest that it differs from the taxa listed in Table 4. The caudal vertebrae of the Toba dinosaur possess following characters: (1) the amphicoelous centrum of cranial caudal, (2) over 1.0 of the length/height ratio of cranial caudal centrum, (3) the ventral excavation (depression) on the cranial caudal centrum bounded by a ventrolateral ridge on each side, and (4) the dorsoventrally compressed cross-section of middle caudal centrum. The combination of the primitive, (1) and (2), and advanced, (3) and (4), characters (Upchurch, 1998) is unique within the Titanosauria, suggesting that Toba dinosaur may represent a new taxon. The discovery of a possibly new titanosaurian dinosaur from the Early Cretaceous of Japan indicates that primitive titanosaurians were more diverse in Asia, and their evolution was more complicated than previously thought.

Barrett *et al.* (2002) described some sauropod teeth from the Lower Cretaceous of central Japan and identified them as Titanosauriformes, gen. et sp. indet. Because Toba dinosaur does not preserve any tooth, it is basically impossible to compare with the material of Barrett *et al.* (2002). With the further discoveries at either locality, it may be possible to compare with each other and discuss more.

Based on the discussion above, it is almost certain that Toba dinosaur is one of the relatively primitive

Table 4. Comparisons of characters between Toba dinosaur and 8 genera within node K of Upchurch (1998) (=Titanosauriformes).
Numbers (129 to 191) represent character numbers (C129 to C191) that Upchurch (1998) described. Data sets other than Toba dinosaur are after Upchurch (1998). Empty cells represent '?'.

	129	130	131	132	136	137	138	144	158	159	186	187	189	190	191
Brachiosaurus	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1
Lapparentosaurus	0	0			0	0	1				1	1	1	1	1
Phuwiangosaurus	0	0	0	1	0		1		1	1	1	1	1	1	1
Andesaurus	0	0	0		0	0	1				1		1		
Malawisaurus	1	1	0	0	0	0	1								
Alamosaurus	1	1	1	0	0	1	1	1							
Opisthocoelicaudia	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Saltasaurus	1	1	1	0	1	1	1								
Toba dinosaur	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1

taxa of Titanosauria, but assignment to any of the family, genus, or species level is not possible currently. Therefore, it can be classified as follows, following to Upchurch *et al*. (2004):

Sauropodmorpha Huene, 1932
Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1986
Titanosauriformes Salgado, Coria, et Calvo, 1997
Titanosauria Bonaparete et Coria, 1993
Fam., gen., et sp. indet.

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일본 중앙 Toba시의 전기 백악기 지층에서 산출된 Titanosaurian 용각류의 부분 골격

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요 약: 일본 중앙의 Toba시에 있는 전기 백악기 (Valanginian~Barremian) Matsuo Group에서 용각류 골격 일부가 발굴되었다. 4개의 꼬리 척추뼈, 오른쪽 왼쪽 상박골과 대퇴골이 인지되었으며 왼쪽 요골과 오른쪽 경골, 오른쪽 비골, 그리고 왼쪽 좌골(?)의 동정은 뼈가 불완전하여 잠정적이다. 이 공룡은 다음과 같은 형태적 특징에 기초해 Upchurch *et al*. (2004)의 분류를 따르면 Titanosauria에 속한 것으로 확인된다. 특징은 (1) 대퇴골의 4th trochanter가 shaft의 안뒤쪽에 위치하며 (2) 상완골과 대퇴골 길이의 비는 대략 0.89 이고 (3) 대퇴골의 상부 좌측 표면이 뚜렷하게 부풀어 있으며 (4) 중간 미추의 신경궁은 추체의 앞쪽에 위치하고 (5) 대퇴골의 단면은 매우 비대칭 (= 2.3)이다. 게다가 미추는 다음과 같은 특징이 있다. (1) 앞쪽 미추의 추체는 amphicoelous이며 (2) 앞쪽 미추체의 길이와 높이의 비는 1.0이 넘고 (3) 앞쪽 미추체의 하부 excavation은 각 양쪽 ventrolateral ridge에 둘러싸여있으며 (4) 중간 미추체의 단면은 위아래로 납작하다. 원시적인 특징 (1)과 (2)와 함께 진화된 특징인 (3)과 (4)의 조합은 Titanosauria 그룹 내에서 독특하며 이 공룡이 새로운 속과 종일 가능성을 암시한다. 일본의 전기 백악기에서 산출된 새로운 가능성이 있는 티타노사우루스류 용각류의 발견은 원시적인 티타노사우루스류가 아시아에 더 다양했으며 이들의 진화가 이전에 생각했던 것보다 더 복잡했다는 것을 지시한다.

주요어: Titanosauria, 전기 백악기, Toba, 일본

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Appendices

Appendix 1.

Characters and character states (in parentheses) obtained from Toba dinosaur. The number in front of the description is same as those of Upchurch (1998).

C129: (0) articulations between cranial caudal centra are amphicoelous,
C130: (0) same as above,
C131: (0) articulation between middle caudal centra are amphicoelous/amphiplatyan,
C132: (0) centrum length divided by centrum height (in the most cranial caudals) is approximately 1.0 or more,
C136: (1) ventral surfaces of cranial caudal centra are mildly or deeply excavated, with the excavation bounded by a ventrolateral ridge on each side,
C137: (1) centra of middle caudals display a dorsoventrally compressed transverse cross-section,
C138: (1) neural arches of middle caudals are situated on the cranial half of the centrum (Although this character is not observable on the middle caudals C and D, it is clear on the last proximal caudal B, and thus C138 should be (1)),
C144: (1) disappearance of caudal ribs occurs on Cds14-16 or more cranially,
C158 and C159: (1) forelimb/hindlimb length ratio is 0.75 or more (These two characters can not be applied directly to Toba dinosaur, but the ratio of (humerus+ulna)/(femur+tibia) does not differ much from that of humerus/femur in sauropods, at least. Because the value (1250/1400 = 0.89) of Toba dinosaur is much larger than 0.75, there should not be any doubt),
C186: (1) femoral shaft is straight (Right femur of Toba dinosaur is slightly curved, but this curvature is a result of deformation caused by diagenesis),
C187: (1) prominent "bulge" on the lateral surface of the femur, near the proximal end present,
C189: (1) fourth trochanter on femur is situated on the caudomedial margin of the shaft,
C190: (1) fourth trochanter is a low rounded ridge,
C191: (1) horizontal cross-section through the femoral shaft is elliptical or subrectangular (with the transverse diameter wider than the craniocaudal diameter).

Appendix 2.

Synapomorphies at each node of the cladogram of Upchurch (1998, figure 19) and in figure 12.

Node A (Sauropoda) (=Sauropoda of figure 12): C144, C186, and C191
Node G (unnamed): C189
Node J ("Brachiosauria") (=Camarasauromorpha of figure 12): C159
Node K (unnamed) (=Titanosauriformes of figure 12): C138, C187
Node O (unnamed) (=probably corresponds to Lithostrotia of figure 12): C129, C130, C132
Node P (Titanosauridae): C137
Node Q (unnamed) (=Saltasauridae of figure 12): C136