NEW TITANOSAURID (DINOSAURIA: SAUROPODA) FROM THE LATE CRETACEOUS OF CENTRAL INDIA

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ABSTRACT—The earliest record of titanosaurids anywhere in the world was established in India in 1877. Further collections from fossiliferous pockets near Jabalpur were made by C. F. Matley during 1917–1919. This material formed the basis of a number of taxa from the Indian Late Cretaceous, even though most of the bones were isolated and fragmented. New titanosaurid skeletal material (collected during 1984–1986) described here represents part of an individual in associated and mostly articulated condition, though skull, hind limb and foot bones are missing. Paucity of associated skeletal remains of titanosaurids anywhere in the world makes the present find valuable in understanding these specialized sauropods. A new taxon, *Titanosaurus colberti*, is erected for the reception of the new material. The genus *Titanosaurus* is diagnosed and three species are identified from India: *T. indicus*, *T. blanfordi*, and *T. madagascariensis*.

INTRODUCTION

The titanosaurids are regarded as the most advanced of the sauropod dinosaurs. Restricted to the Cretaceous, they were first recorded from the Lameta Formation of central India (Falconer, 1868; Lydekker, 1877, 1879). The Lameta Formation occurs mostly as disconnected patches below the Deccan Trap volcanic suite and rests above the Precambrian or Gondwana rocks. It is best developed and exposed in its type area near Jabalpur, in the eastern part of the Narmada Valley (Fig. 1). The early titanosaurid discoveries from the type area and another locality near Pisdura, some 320 km south of Jabalpur (Fig. 1), were mainly due to the efforts of British explorers during the last century. The fossil material in all such cases was rather fragmentary—yet Lydekker (1877, 1879) was able to erect two titanosaurid species. Falconer (1868) first described two caudal vertebrae from Jabalpur and accurately figured one of them, although he did not assign any name to these vertebrae. Lydekker (1877) designated them as *Titanosaurus indicus*. Later Lydekker (1879) erected another titanosaurid species, *Titanosaurus blanfordi*, from Pisdura.

After a gap of nearly four decades, Matley (1921, 1923) carried out extensive work and recognized three distinct dinosaur-bearing horizons in the sediments of the Lameta Formation of Jabalpur (Huene and Matley, 1933). These are (i) carnosaur beds, (ii) ossiferous conglomerate and (iii) sauropod beds. The last pocket yielded the maximum number of well-preserved titanosaurid skeletal elements. Huene and Matley (op. cit.) made a detailed study of the collection including those known earlier and identified *Titanosaurus indicus* and *Antarctosaurus septentrionalis* from the Lameta Formation of Jabalpur. Matley (1921) also recovered some more titanosaurid bones from Pisdura and designated these as *Titanosaurus blanfordi*, *T. indicus*, and *Laplatasaurus madagascariensis* (Huene and Matley, 1933).

Work in the sediments of the Lameta Formation near Pisdura was taken up by a team of workers of the Geological Studies Unit, Indian Statistical Institute, in the early sixties. In addition to Pisdura, the team also began work in a nearby locality near Dongargaon, 16 km south-east from Pisdura (Fig. 1), already known to contain fishes and gastropods (Woodward, 1908; Matley, 1923). Exploration around Dongargaon during 1968–1969 was rewarded by the recovery of well preserved dinosaur bones. A well-preserved dinosaur braincase from this collection was described by Berman and Jain (1982), who assigned it to the Family Titanosauridae but did not refer it to any genus or species.

During three field seasons from 1984 to 1986, excavations at Dongargaon by a team led by one of the authors (SLJ) produced a quite well-preserved, partly articulated skeleton of a titanosaurid. The assemblage included vertebrae and ribs from different regions of the axial skeleton, a scapula and a coracoid both from the left side, part of a left forelimb, and a co-ossified sacrum articulated/associated with the pelvis on both sides. A few caudal vertebrae were also found lying on the surface near the articulated pelvis. Bones were found to be concentrated in an excavated area of approximately 23 × 8 m (Fig. 2A). Attempts to extend the excavation for more bones were not successful. Significantly no skeletal elements other than those mentioned above were found. The association strongly suggested the presence of a single individual. The present paper describes this new titanosaurid material.

GEOLOGY, FAUNA AND AGE

The Lameta Formation of Dongargaon comprises red and green silty clays overlain by variegated finely laminated clays intercalated with thin partings of claystone, limestone, marl, and occasional sandstone partings (Mohabey et al., 1993). The total thickness of the formation is approximately 20 m. The sediments of the Lameta Formation are in general considered to be of fluvio-lacustrine origin on the basis of the presence of freshwater and terrestrial invertebrate and vertebrate remains, as well as sedimentological analysis (Hislop, 1859; Huene and Matley, 1933; Jain and Sahni, 1983; Pascoe, 1964; Sahni and Mehrotra, 1974; Brookfield and Sahni, 1987; Tandon et al., 1990). A fresh water environment for the Lameta sediments of Dongargaon was also proposed by Mohabey et al., (1993).

It has already been mentioned that the fauna of the Lameta Formation of Dongargaon include some fishes (*Eoserranus hislopi*, *Lepisosteus indicus*, and *Pycnodus lametae*) and gastropods (Woodward, 1908); however, the exact stratigraphic level of these fish finds is not very clear. During the last decade some reptilian remains came to light from the lower green clays. A titanosaurid braincase (Berman and Jain, 1982) and a pelomedusid carapace and plastron (Jain, 1986) have since been added. It may be mentioned that a pelomedusid skull is also known from Pisdura; this latter skull and the plastron and carapace from Dongargaon belong to the same taxon, *Shweboemys pisdurensis*. Recently, Mohabey et al. (1993) recorded the presence of dinosaur bones and eggshells and crocodile scutes from

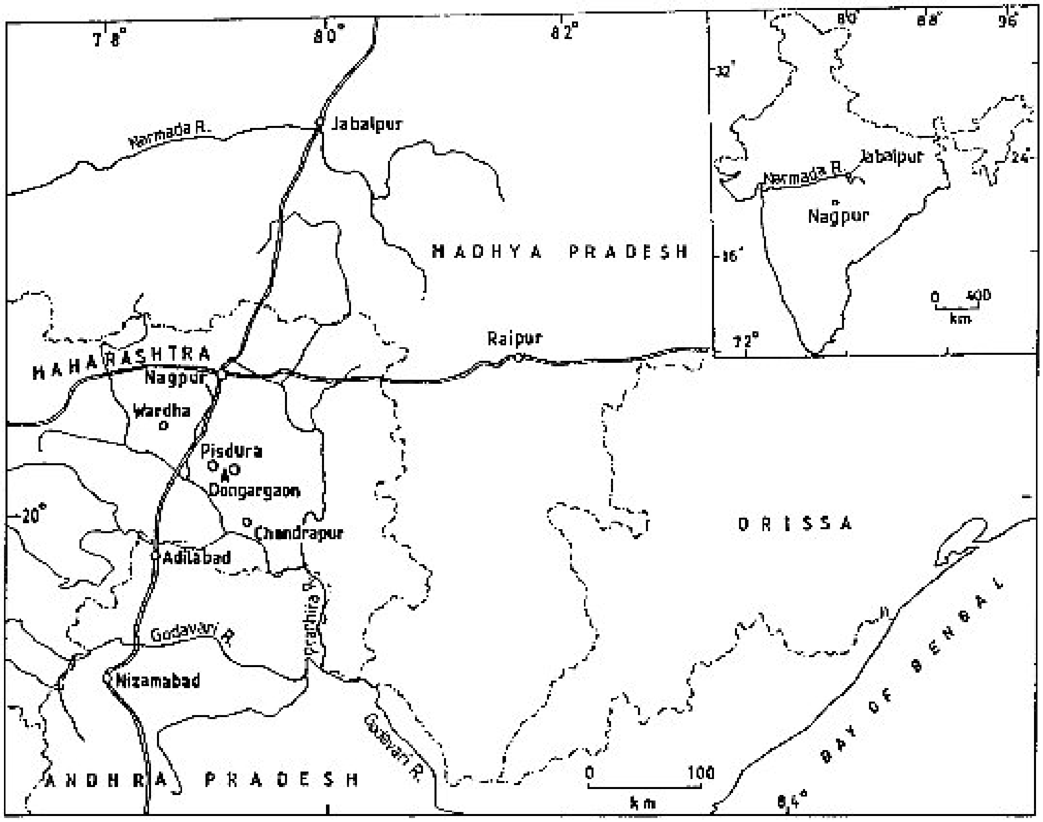

FIGURE 1. Map showing the new fossil locality (Δ).

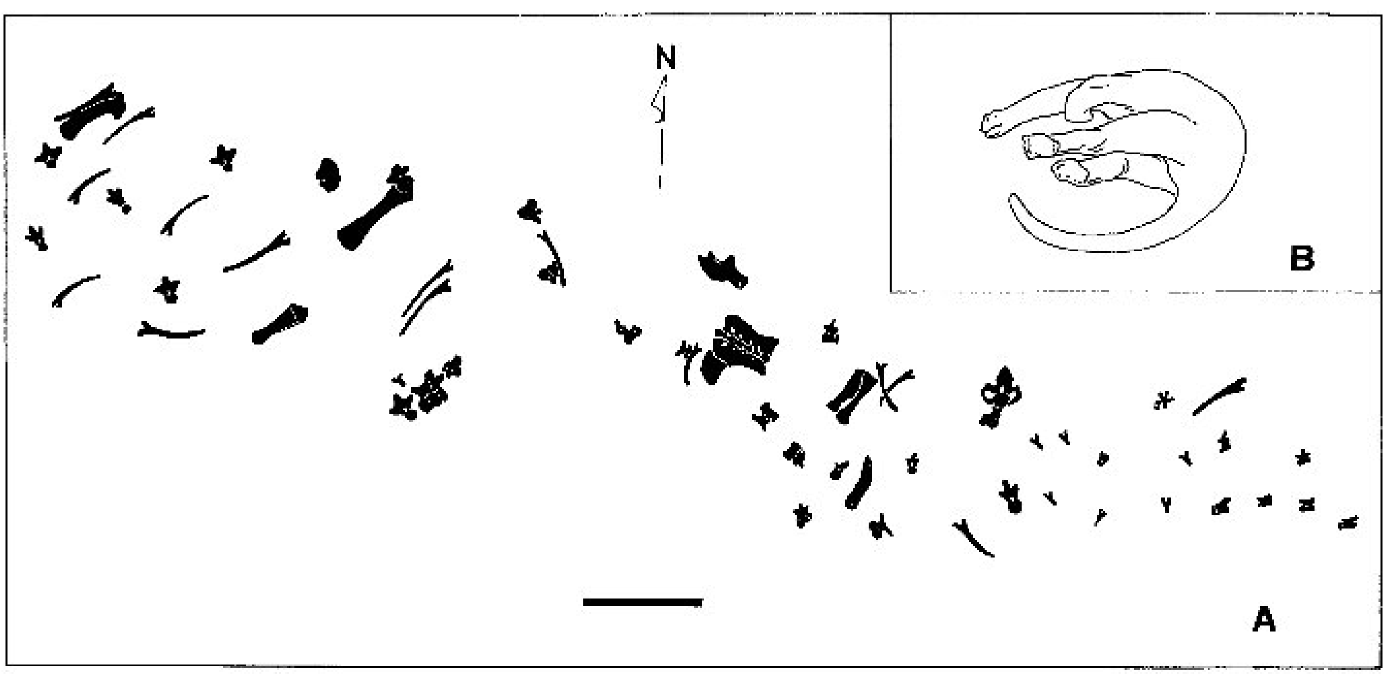

FIGURE 2. **A**, distribution of the fossil bones of *Titanosaurus colberti* represented by a single individual. Scale bar equals 2 meters. **B**, the hypothesized orientation of the animal at burial.

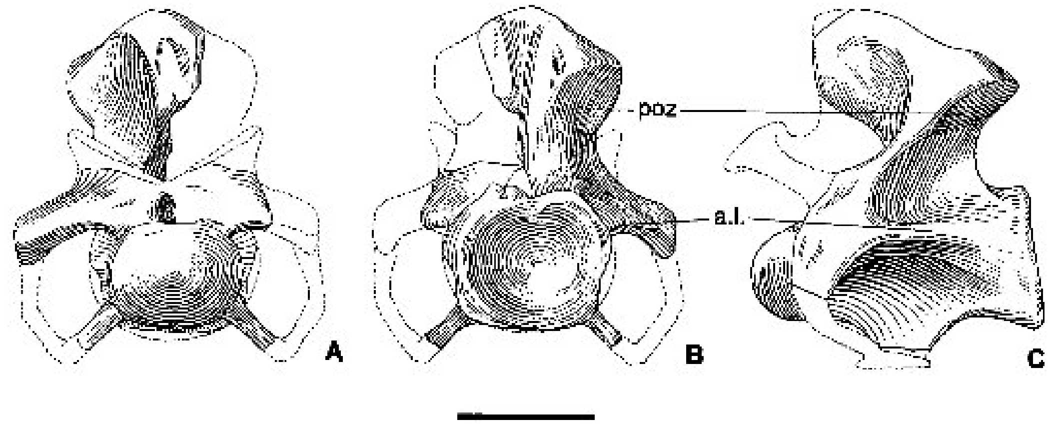

FIGURE 3. Anteriormost cervical vertebra of *T. colberti* (ISIR335/1) in, A, anterior; B, posterior; and C, lateral views. **Abbreviations: a.l.**, accessory lamina; **poz**, postzygapophysis. Scale bar equals 10 cm.

Dongargaon. They also reported the occurrence of additional fishes, gastropods, pelecypods, and ostracods.

Woodward (1908), while describing the above-mentioned fishes from Dongargaon, placed the age of the fish fauna between Paleocene and Eocene. Matley (1921) also considered the age of the Lameta Formation of Dongargaon as post-Cretaceous. Berman and Jain (1982) considered a Santonian to Maastrichtian range; this view was further supported by Jain (1986) with the description of the pelomedusid skull from Dongargaon. Recently, Mohabey et al. (1993) reviewed the biota of the Lameta Formation of Dongargaon and suggested a terminal Cretaceous (=Maastrichtian) age. The new titanosaurid, described in this paper, is quite an advanced form and when compared with other coeval titanosaurids strongly points to a Maastrichtian age. A Maastrichtian age for the Lameta Formation, in general, is also suggested by Buffetaut (1987), Dogra et al. (1988), Udhoji and Mohabey (1991), and Chatterjee (1992).

MATERIAL

The new titanosaurid bones were excavated from the green clays of the Lameta Formation of Dongargaon. The articulated/associated nature of the skeleton (Fig. 2A) clearly indicates that the animal was buried without being transported far from the site where it died. However, the absence of any hind limb with the articulated pelvis and sacrum is rather unfortunate. It is difficult to conclude whether the hind limbs were present initially but were lost or removed from the association due to recent erosion or whether they were disarticulated/dismembered before burial. From the occurrence of the bone association (which was basically a partial carcass), it appears that the former suggestion is more applicable. An attempt has been made (Fig. 2B) to suggest the probable posture of the animal at the time of burial. The size and the osteological characters of the bones also point to the fact that all the recovered bones represent a single individual.

The new material includes nine cervicals (ISIR335/1–9), seven dorsals (ISIR335/10–16), fourteen ribs (ISIR335/17–30), a complete sacrum with six co-ossified vertebrae and ribs (ISIR335/31), sixteen caudals (ISIR335/32–47), nine chevrons (ISIR335/48–56), a left scapula (ISIR335/57) and a left coracoid (ISIR335/58), a left humerus and a left ulna (ISIR335/59–60), a pair of ilia (ISIR335/61–62), a pair of pubes (ISIR335/63–64) and a right ischium (ISIR335/65), making a total of 65 bones.

SYSTEMATIC PALEONTOLOGY

Order Saurischia Seeley, 1888
Suborder Sauropodomorpha Huene, 1932
Infraorder Sauropoda Marsh, 1878
Family Titanosauridae Lydekker, 1885
Genus *Titanosaurus* Lydekker, 1877

Titanosaurus colberti, sp. nov.

Holotype—ISIR335/1–65: a partial skeleton. Palaeontological Collection, Geology Museum, Indian Statistical Institute, Calcutta (ISI).

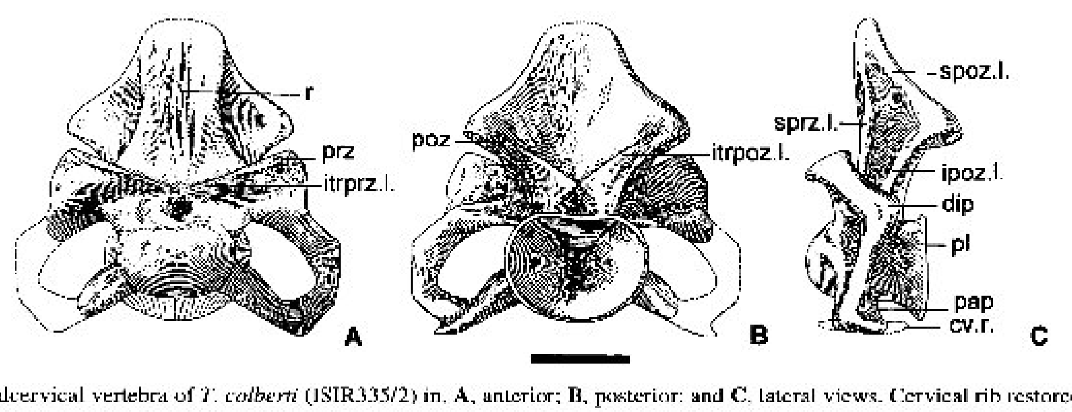

FIGURE 4. Midcervical vertebra of *T. colberti* (ISIR335/2) in, A, anterior; B, posterior; and C, lateral views. Cervical rib restored from ISIR335/3. **Abbreviations: cv. r.**, cervical rib; **dip**, diapophysis; **ipoz. l.**, infrapostzygapophyseal lamina; **itrpoz. l.** intrapostzygapophyseal lamina; **itrprz. l.**, intraprezygapophyseal lamina; **pap**, parapophysis; **pl**, pleurocoel; **poz**, postzygapophysis; **prz**, prezygapophysis; **r**, ridge; **spoz. l.**, suprapostzygapophyseal lamina; **sprz. l.**, supraprezygapophyseal lamina. Scale bar equals 20 cm.

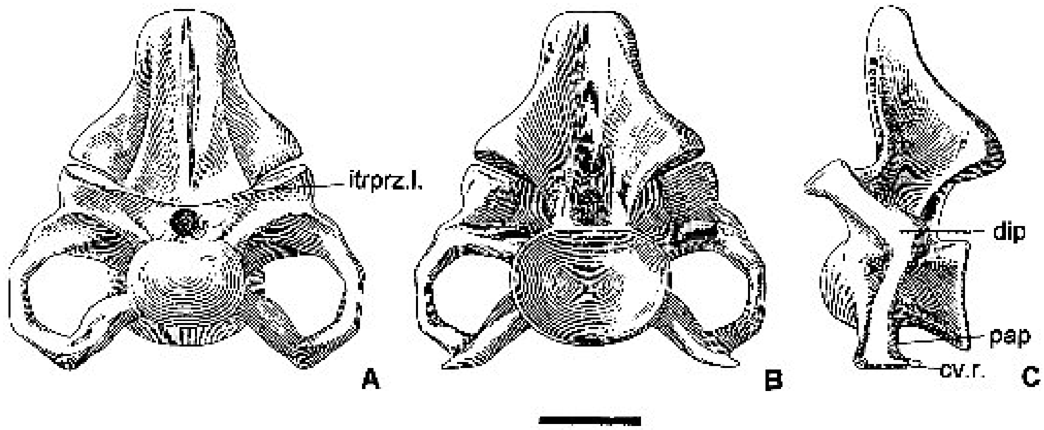

FIGURE 5. Posterior cervical vertebra of *T. colberti* (ISIR335/8) in, **A**, anterior; **B**, posterior; and **C**, lateral view. Restored after ISIR335/3. **Abbreviations: cv.r.**, cervical rib; **dip**, diapophysis; **itrprz. l.**, intraprezygapophyseal lamina; **pap**, parapophysis. Scale bar equals 20 cm.

Horizon and Locality—Lameta Formation of Wardha Valley; Dongargaon village; Chandrapur district, Maharashtra, Central India.

Age—Late Cretaceous (Maastrichtian).

Etymology—Species named in honor of Prof. Edwin H. Colbert, foremost exponent of dinosaurs.

Diagnosis—Large, advanced titanosaurid (as diagnosed by McIntosh 1990a) with strongly procoelous caudals throughout; cervicals and dorsals strongly opisthocoelous with well-marked pleurocoels; cervical centra small; transverse process of cervicals wide, directed laterally and robust in shoulder region; neural spines of medium height, not bifid, directed more posteriorly in dorsals; transverse processes of dorsals robust, projected laterally and a little upward; sacrum comprising of six co-ossified vertebrae and ribs; anterior face of the first sacral (second dorsosacral) centrum and posterior face of the last sacral (sacrocaudal) centrum convex; sacricostal yoke well developed; first sacral rib moderately developed extending outward; chevron facets on anterior rim of midcaudals located on raised prominent ridges but on low, faint ridges on posterior rims; middle part of the caudal centra flat ventrally, without any ridge; chevron facets located on very low ridges in the distal caudals; scapula broad; preacetabular process of the ilium directed strongly outward; ischium flat, bladelike, transversely expanded in the middle; pubis robust; ulna robust and triangular in cross section.

OSTEOLOGICAL DESCRIPTION

The Vertebral Column

The vertebral count in most titanosaurids is not known. However, in the Argentinian *Saltasaurus loricatus*, there are about 23 presacral and about 35 caudal vertebrae (Powell, 1986:fig 1). In *Titanosaurus colberti*, the exact vertebral count also remains unknown. The following description is based on 38 collected vertebrae of which six sacrals are coossified. The last cervical and the three anteriormost dorsals were found articulated. There is another association of four articulated distal caudals. All other vertebrae were excavated as isolated segments.

Cervical Vertebrae (Figs. 3, 4, 5, 6)—There are nine cervicals in the collection. The atlas-axis complex is not preserved. Out of these, ISIR335/1 appears to be the anteriormost (third/fourth) cervical. ISIR335/2, ISIR335/3 and ISIR335/4 are midcervicals while ISIR335/8 and ISIR335/9 are posterior cervicals. However, due to distortion it is not possible to fit them perfectly all together.

The cervical centra are all strongly opisthocoelous, small, constricted in the middle, and successively increase in length. These are marked by relatively small, elongated pleurocoels, opening quite high on the centra. The anteriormost cervical centrum (Figs. 3, 6A, B) has a strong, hemispherical, convex, anterior articular surface; the rest are transversely elliptical from midcervicals to posterior cervicals. The anterior convexity also becomes reduced in successive cervicals. The posterior concave surfaces are considerably larger with pronounced rims. The strongly developed parapophyses are consistently placed low on the anterior rim of the centra throughout the cervical region. From midcervical onwards, the parapophyses expand backward covering a considerable portion of the lower part of the centra. The parapophyses are directed outward and downward (Figs. 4, 5); the terminal faces are coplanar with the ventral surfaces of the centra.

The transverse processes are directed laterally and become quite wide from midcervical onwards (Figs. 4, 5, 6C–F); posteriorly, near the shoulder region they are widest (Table 1). The well-developed diapophyses are small in the anteriormost cervical but become somewhat larger and stouter from the midcervicals backwards, projecting outward and a little upward. The prezygapophyses are widely divergent in the mid- and posterior cervicals, supported by supraprezygapophyseal laminae. The postzygapophyses are high and supported by infrapostzygapophyseal laminae. Infra- and suprapostzygapophyseal laminae form a deep cavity. Intraprezygapophyseal and intrapostzygapophyseal laminae are present in the midcervical vertebrae (Fig. 4); in the posterior cervicals, only the intraprezygapophyseal lamina can be seen (Fig. 5). The neural canal is uniformly rounded in the cervical series. The neural spines are single, moderately high, and are slightly swollen at their tips with a prominent anterior vertical ridge. Laterally the spines are crossed by anterior and posterior diapophyseal laminae.

Cervical Ribs (Figs. 4, 5)—The double-headed cervical ribs are firmly coalesced with the diapophyses and parapophyses and lie slightly below the axis of the vertebral column. The cervical ribs are placed parallel to the axis of the vertebral column. Though the ends are broken in most of the specimens, in the midcervicals an anterior projection is prominent at the junction of the tuburculum and capitulum. The posterior projections are also not well preserved but are present in both midcervicals as well as in the posterior cervicals.

Dorsal Vertebrae (Figs. 7A–E, 8, 9A–C)—There are seven dorsal vertebrae of which five are better preserved. Of the better preserved, the first three dorsals (ISIR335/10, ISIR335/11 and

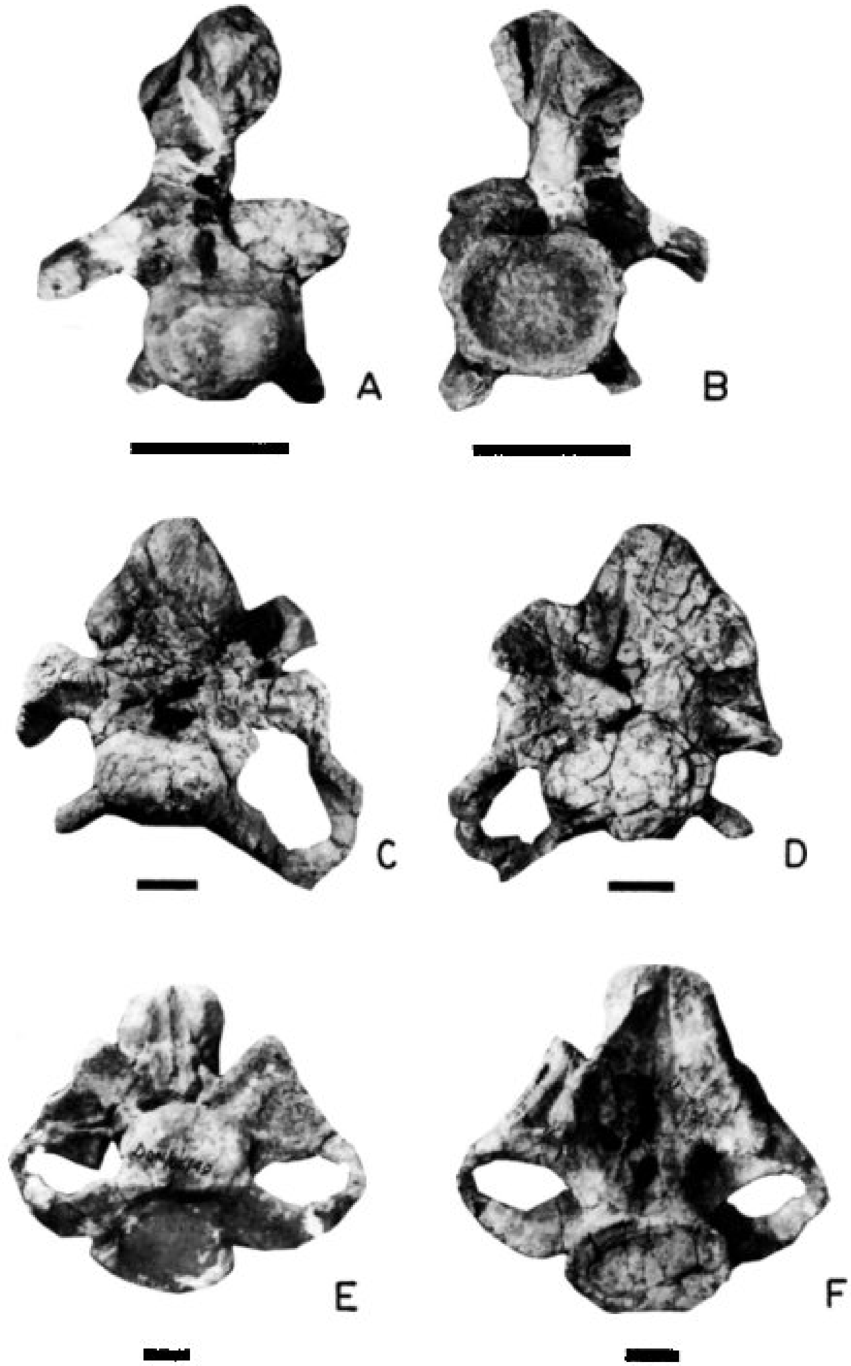

FIGURE 6. A, B, anterior and posterior views of an anterior cervical vertebra (ISIR335/1). C, D, anterior and posterior views of a midcervical vertebra (ISIR335/2). E, F, anterior and posterior views of a posterior cervical vertebra (ISIR335/8). Scale bars equal 10 cm.

ISIR335/12) were found articulated with the last cervical (ISIR335/9) (Fig. 7A). The two others, ISIR335/15 and ISIR335/16, are both middorsals. The damaged dorsals are not considered further. The measurements of the dorsal vertebra are given in the Table 1.

The centra of all the dorsal vertebrae are strongly opisthocoelous. The anterior surfaces of the centra are hemispherical; the posterior concavity is larger than the anterior convexity. The centrum length decreases in successive dorsals; however, there is an abrupt change in centrum length between the first and second dorsals, which may be an artifact of preservation. Deep, slitlike pleurocoels occur on the lateral faces just below the neural arches. The neural arches and the neural spine together cover two-thirds of the total vertebral height in all the available dorsals. The neural arches are quite wide in the anterior dorsals (Figs. 7B–C, 8). The neural canal is large and rounded. The transverse processes are robust and directed laterally and a little upward. The width across the transverse processes is larger in the anterior dorsal but reduces in the middorsal region (Table 1). The articular facets on the transverse processes are quite prominent in all the dorsals. There is a gradual change in the position of the parapophyseal facets from the anterior to the middorsals. These are placed high on the anterolateral corner of the centrum in the first dorsal

TABLE 1. Measurements (centimeters) of the presacral and caudal vertebrae of *T. colberti*.

Registration nos.	Maximum length of centra	Maximum diameter of the posterior face of the centra	Maximum width (across transverse process)	Greatest overall height
Anteriormost cervical ISIR335/1	22	12		26.5
Midcervical ISIR335/2	24	28	58*	50*
Posterior cervical ISIR335/8	26**	28	70	70
First dorsal ISIR335/10	28	19	55	55
Second dorsal ISIR335/11	16	20	60	60
Third dorsal ISIR335/12	24	20	50*	48
Middorsal ISIR335/15	22	22	35**	60
Middorsal ISIR335/16	19	21*	45*	62
Proximal caudal ISIR335/32	25	10*	—	35
Proximal caudal ISIR335/33	24**	12	—	45
Midcaudal ISIR335/42	18	10*	—	28
Midcaudal ISIR335/43	17	—	—	25
Distal caudal ISIR335/44	15	8.5	—	18
Distal caudal ISIR335/45	15	8.5	—	17*
Distal caudal ISIR335/46	13	6.5	—	14*
Distal caudal ISIR335/47	12.5	7	—	13*

*Estimated and/or restored in figures.
**Compressed and/or distorted.

(ISIR335/10). However, the parapophyses move further upward on the neural arch and occur close to the diapophyses in the middorsal region (Figs. 7D, E, 9A–C). The two articular facets, which are quite widely spaced in the anterior dorsals, move closer in the middorsals; these are more or less of the same size. There are three laminae on the transverse processes. The centrodiapophyseal lamina extends from the diapophyses downward and joins with the infrapostzygapophyseal lamina, which again extends from the postzygapophyses downward to the floor of the neural canal (Fig. 9A–C). The postzygodiapophyseal lamina is directed backward to the postzygapophysis, and the supradiapophyseal lamina is directed upward to the spine (Fig. 9A–C). The prezygodiapophyseal lamina is not prominent in any of the dorsals. The centrodiapophyseal, postzygadiopophyseal, and infrapostzygapophyseal laminae together form the strong, deep, lateral infradiapophyseal cavity. The supradiapophyseal lamina together also constitute the deep supradiapophyseal cavity. The prezygapophyses are placed quite wide apart in the anterior dorsals, but in the middorsals they are placed closer to the midline. The postzygapophyseal facets also change accordingly from anterior dorsals to middorsals; these facets are spatula-shaped in the middorsals. There is no hyposphene-hypantrum in any of the collected dorsals. The undivided neural spine is of medium height with prominent vertical ridges. The spine is oriented perpendicular to the neural canal but slightly inclined backward.

Thoracic Ribs (Fig. 9D)—Of the 14 collected ribs, eight are sufficiently preserved to permit length measurements. In centimeters, they are 120, 116, 100, 95, 90, 78+, 77+, and 63+. All the ribs display the characteristic curvature right up to the capitulum and tuberculum. Among them, three, ISIR335/17, ISIR335/21, and ISIR335/30, are quite stout and proximally curved indicating anterior dorsal ribs. The tuberculum and the capitulum are of subequal size, subrounded, and are marked with a notch in between. The tuburcular surface is slightly elongated and oval, while the capitulum is nearly rounded. There is a marked ridge running along the length of the rib shaft bifurcating just before the proximal notch and terminating toward the end of the capitulum and tuberculum. Medially there is a marked depression running anteriorly. The proximal part of the rib is concavo-convex in cross section and distally plano-convex.

Sacrum (Figs. 7F and 10)—The sacrum (ISIR335/31) was found coossified along with the left ilium, while the right ilium was found articulated but not coossified with the sacrum. The whole block, especially the anterior part, apparently underwent dorsoventral compression resulting in flattening of the sacrum and ilia. It was exposed on its dorsal side where it was also quite compressed. The coossified sacrum consists of six vertebrae of which the first two have been identified as dorsosacrals and the last, a sacrocaudal. The latter is most probably biconvex. The centrum of the first sacral (second dorsosacral) is opisthocoelous; the anterior surface of the centrum is oval in outline. The posterior convexity of the last sacral (sacrocaudal) centrum is less pronounced than in the first sacral. The fourth, fifth, and the last sacral centra are narrower ventrally than the first three sacrals. The fourth and the sixth sacral centra appear to be more elongated than the others. The ventral surfaces of the centra are somewhat flattened with a longitudinal depression. Pleurocoels are not present in any sacral vertebrae.

Except one, the neural spines are not preserved. The neural arches are slightly compressed dorsally but the fact that these were not very high is indicated by the better preserved second neural arch and part of the preserved neural spine. The broken neural spine is not bifid and appears to be of medium height with an anterior vertical ridge and posterior rugosities. Though the neural canal is not clearly visible anteriorly or posteriorly, it appears to be rounded.

The first sacral rib is moderately developed, narrow dorsally but slightly expanded ventrally, and fused with the centrum. Though the distal end is broken, it may not have participated in the formation of the sacricostal yoke. It is extended distally and reaches the ilium. The second to sixth sacral ribs are quite robust; the third and the sixth are stouter than the others. Proximally, these five ribs are fused with their respective centra; the middle three are, however, slightly expanded anteroposteriorly. Dorsally, each rib has winglike robust expansions that arise from the neural arches. Distally, these five ribs are much expanded and are completely fused with one another. The distal ends of the second to fifth sacral ribs are fused with each other; their fusion lines are prominent. These five ribs enclose four sacral cavities on each side; dorsally these cavities are wider than their ventral extensions.

Actual measurements (centimeters) of the sacrum are as follows: total length 105, anterior width (across the second sacral ribs) 72, mid-width (across the third sacral ribs) 78 and posterior width (across the sixth sacral ribs) 85; length of individual centra from the first to sixth sacral: 13, 13, 20, 18, 14, and 17, respectively; maximum diameters of the anterior face of the first sacral and the posterior face of the sixth sacral: 24 and 21, respectively.

Caudal Vertebrae (Figs. 7G–I, 11, 12, 13, 14, 15, 16A–F)—The collection includes sixteen caudals of which nine are well preserved. ISIR335/34 (found near left pubis), ISIR335/35

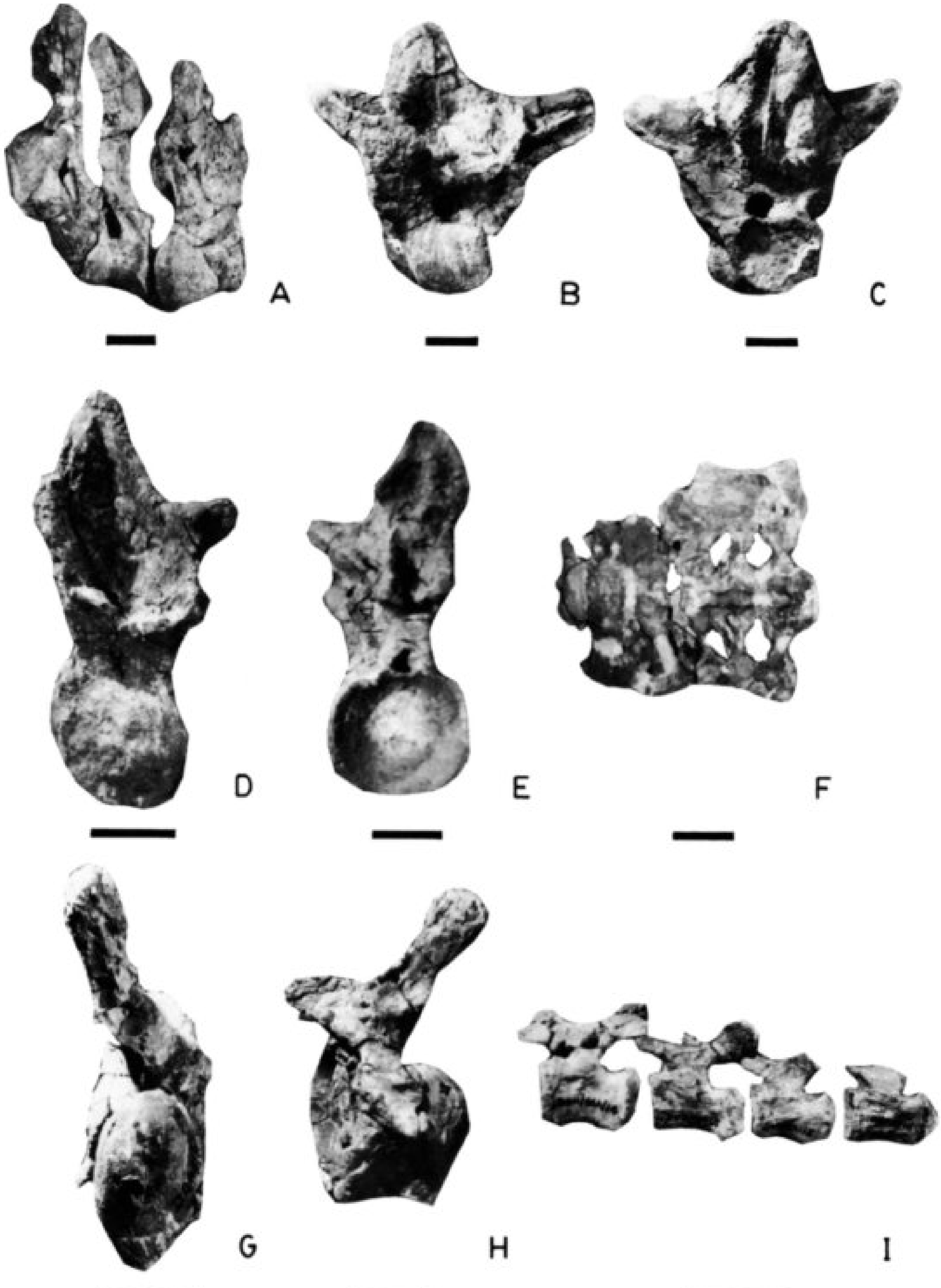

FIGURE 7. **A**, articulated first, second and third dorsal vertebrae (ISIR335/10, ISIR335/11 and ISIR335/12 respectively). **B**, **C**, anterior and posterior views of a second dorsal vertebra (ISIR335/11). **D**, **E**, anterior and posterior views of a middorsal vertebra (ISIR335/15). Scale bars equal 10 cm. **F**, ventral view of the sacrum (ISIR335/31). Scale bar equals 25 cm. **G**, **H**, posterior and lateral views of a proximal caudal vertebra (ISIR335/33). **I**, articulated distal caudals (ISIR335/44, ISIR335/45, ISIR335/46, ISIR335/47 respectively). Scale bars equal 10 cm.

(found near the sacrum), ISIR335/32, and ISIR335/33 are proximal caudals; ISIR335/42 and ISIR335/43 are midcaudals, while ISIR335/44, ISIR335/45, ISIR335/46 and ISIR335/47 are articulated distal caudals (Fig. 7I). Extreme distal caudals were not found.

All the caudal vertebrae are remarkably procoelous throughout the series. Both the height and the length of the caudals progressively reduce from the proximal to the distal caudals. However, the height reduces more than the length (Table 1). The anterior concave articular surfaces of the centra are quite deep with distinct rims and they are well-rounded, especially in the midcaudals and the distal caudals (Figs. 11, 12, 13). The

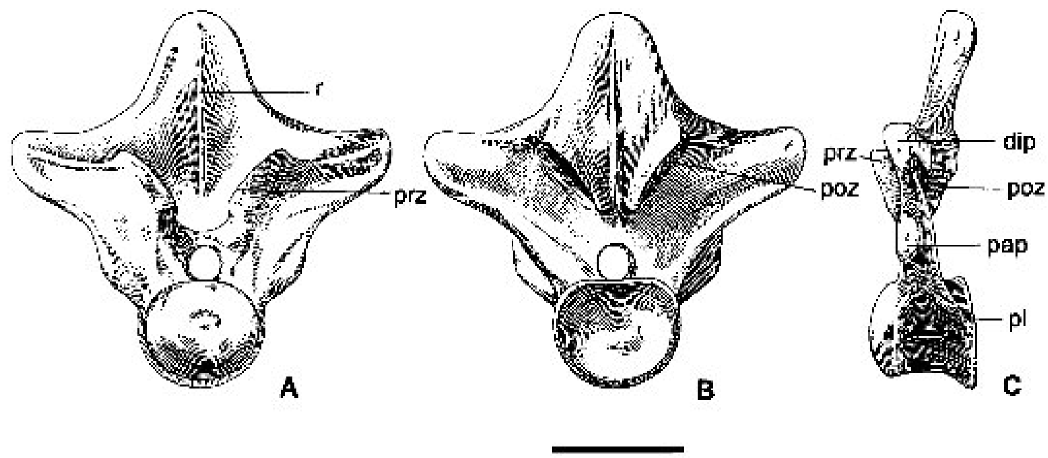

FIGURE 8. Second dorsal vertebra of *T. colberti* (ISIR335/11) in, **A**, anterior; **B**, posterior; and **C**, lateral views. **Abbreviations: dip**, diapophysis; **pap**, parapophysis; **pl**, pleurocoel; **poz**, postzygapophysis; **prz**, prezygapophysis; **r**, ridge. Scale bar equals 20 cm.

posterior convex surfaces are strongly pronounced, cone-like, and somewhat rectangular in the midcaudals and distal caudals due to the development of facets for the chevrons (Figs. 13, 14). Transverse and vertical diameters of the anterior and posterior articular surfaces of the centra are more or less equal. The distal caudal centra are a little constricted. Chevron facets occur on both the anterior and posterior margins of the ventral rim of the centra of midcaudals and distal caudals. In the midcaudals, the chevron facets on the posterior rim are located on a raised prominent ridge; but the chevron facets on the anterior rims are located on comparatively very low, faint ridges (Fig. 12). In the distal caudals, however, the chevron facets, both on the anterior and posterior rims, are situated on very low and faint ridges (Figs. 13, 14, 15, 16A–F). These facets are incipient in the middle part of the ventral surfaces where the centra are waisted and flat (Figs. 14, 15).

The neural arch is lower in the proximal caudals than in the dorsal vertebrae (Fig. 7 G, H). The height of the arch progressively decreases from the midcaudals to the distal caudals. An interesting feature is the position of the neural arch on the elongated centra of the midcaudals and distal caudals. This is related to the conspicuous gaps on the dorsal surface of the centra, and the neural arch is situated so as to accomodate the enlarged pre- and postzygapophyses (Fig. 7I). Prezygapophyses are rod-like, strongly developed with spatulate articular facets in all the caudals and extend well beyond the anterior margin of the centra. Prominent articular facets of the postzygapophyses are also spatulate but small. The rounded neural canal is well marked in all the caudals. The neural spines of the proximal caudals are narrow and slightly swollen at their tips; these are strongly oriented backward. The midcaudal spines appear to be laterally compressed and directed posteriorly. These gradually diminish in size.

Prominent rib facets occur at the junction of the centrum and the neural arch in the proximal caudals only (Figs. 11, 7H). In the mid- and the distal caudals the lateral surfaces are swollen at the junction of the centrum and the neural arch. There are no co-ossified caudals in the collection.

Chevrons (Figs. 16G, H, 17)—Nine chevrons were collected, as listed. Of these, five were examined in detail measuring (in centimeters) 40, 33, 32, 29, and 23 in length. The chevrons are stoutly built with strongly developed hemal arches. The chevrons of the proximal region are robust and more or less circular in cross section. Each chevron has a marked curvature directed posteriorly. The proximal (articular) ends are expanded; the slipper-shaped articular facets have two clearly marked articulating surfaces (anterior and posterior) for the hemapophyses of preceeding and succeeding (adjacent) vertebrae. The hemal canal below the head is quite large and entirely open, as is typical in titanosaurids. Below the canal, the hemal arches coalesce together giving a rounded shape in cross section. Further down, they form a transversely compressed hemal spine with a clearly marked ridge both anteriorly and posteriorly. The size range of the collected chevrons indicates that these belong to the caudal vertebrae from anterior to midcaudal.

Pectoral Girdle

The pectoral girdle is represented by a scapula, ISIR335/57, and a coracoid, ISIR335/58, both from the left side. These were not fused, and they were collected 3 meters apart (Fig. 2A). No sternal plate was found.

Scapula (Figs. 16I, 18)—The scapula is relatively well preserved, broadly expanded both proximally and distally, the breadth being about one-half of the total length of the bone (Table 2). The width of the proximal end is somewhat narrower. From end to end, the scapula has a pronounced anterior curvature (possibly following the contour of the ribs), but it is almost straight along the posterior border. The external surface of the scapular blade is strongly convex, while the internal surface is concave. The shaft of the blade has, however, been flattened a little during preservation, there being no sign of any transverse ridge. The ridge is not pronounced in other titanosaurid genera e.g., *Saltasaurus*. The distal end of the scapula is rugose and developed into an area for the attachment of the muscles over almost the entire width. It is bordered by a curved ridge. The posterior end of the distal portion is thickened transversely making a spoon-shaped glenoid.

Coracoid (Figs. 16I, 19)—The coracoid is comparatively well preserved and complete; it is subrectangular in outline measuring 48 by 32 cms. The anteromedial border is almost straight and thickened, while the remaining part is almost oval. It is irregularly convex on the lateral surface and concave on the inner surface. The coracoid is thickened proximo-medially into a lip-shaped facet for the glenoid, where it is highly rugose. It is perforated by a large elliptical foramen passing through the bone and emerging on the inner side.

Forelimb

The forelimb in our collection is only represented by a well-preserved humerus (ISIR 335/59) and an ulna (ISIR 335/60),

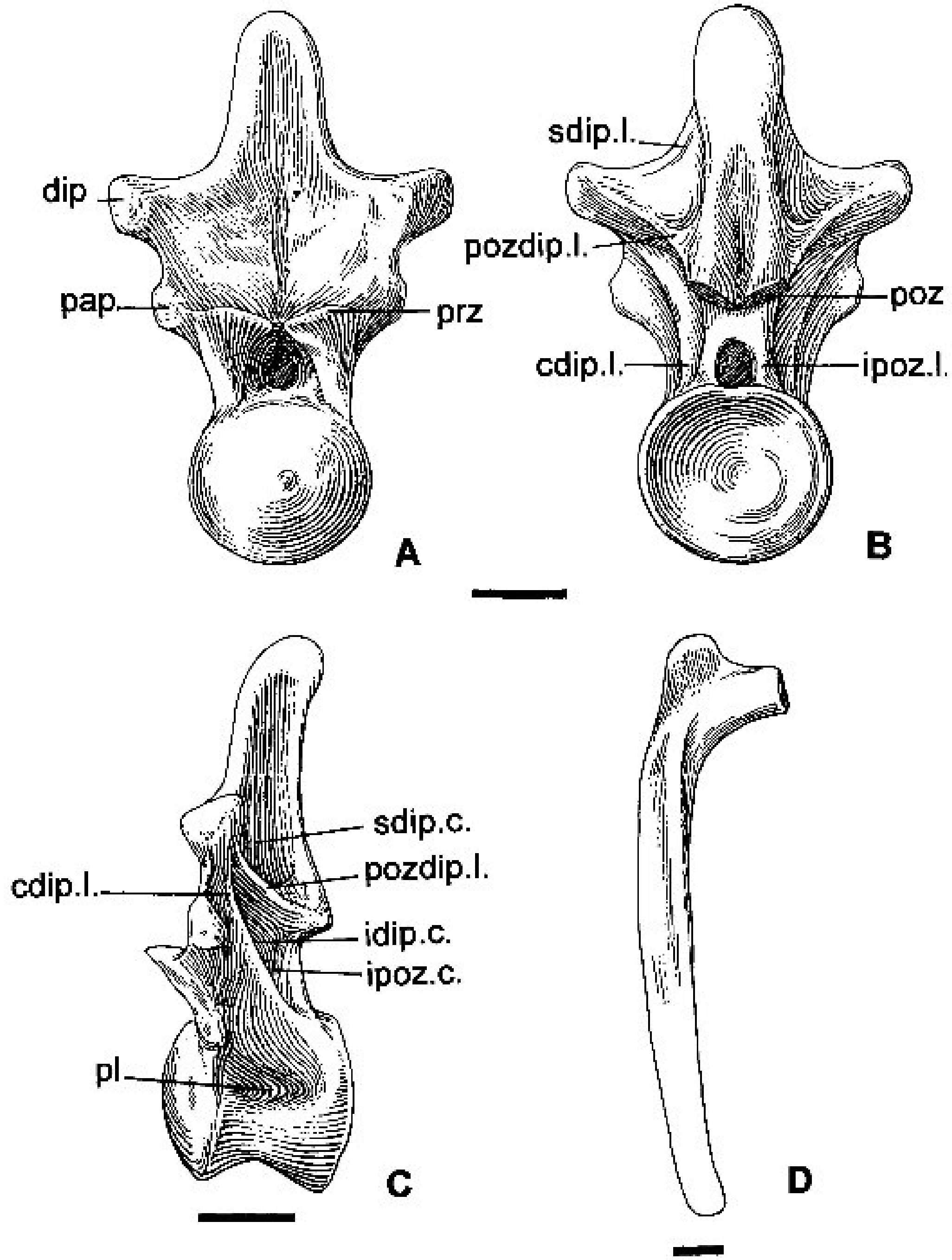

FIGURE 9. **A–C**, middorsal vertebra of *T. colberti* (ISIR335/15) in. **A**, anterior; **B**, posterior; and **C**, lateral views. **Abbreviations: cdip. l.**, centrodiapophyseal lamina; **dip**, diapophysis; **idip. c.**, infradiapophyseal cavity; **ipoz. l.**, infrapostzygapophyseal lamina; **pap**, parapophysis; **pl**, pleurocoel; **poz**, postzygapophysis; **pozdip. l.**, postzygapodiapophyseal lamina; **prz** prezygapophysis; **sdip. c.**, supradiapophyseal cavity; **sdip. l.**, supradiapophyseal lamina. **D**, anterior view of right anterior thoracic rib (ISIR335/17). Scale bar equal 10 cm.

both from the left side. No carpals or phalanges have been found.

Humerus (Figs. 20, 21A, B)—The humerus has a constricted shaft with expanded ends. It appears that the shaft of the bone was somewhat flattened during preservation. The proximal and distal ends are roughly of equal dimensions in contrast with most other titanosaurids (Table 3). The deltoid ridge is prominently developed extending from the proximal end along the anterior external border. The anterior surface of the upper one-third of the humerus is broadly hollowed out, and pronounced rugosities occur over the proximal end. Due to flattening of the entire length of the humerus, the features of the distal end are somewhat obliterated. However, it is rugose and it is marked by a depression posteriorly dividing it into two condyles. The scapula/humerus length ratio in *T. colberti* is 15:11. We also collected a titanosaurid humerus from the Pisdura locality; its measurements are included in Table 3.

Ulna (Figs. 21C, D, 22)—The ulna was found at a distance of about one meter from the humerus. It is well preserved, robust, and does not show any sign of compression. The prox-

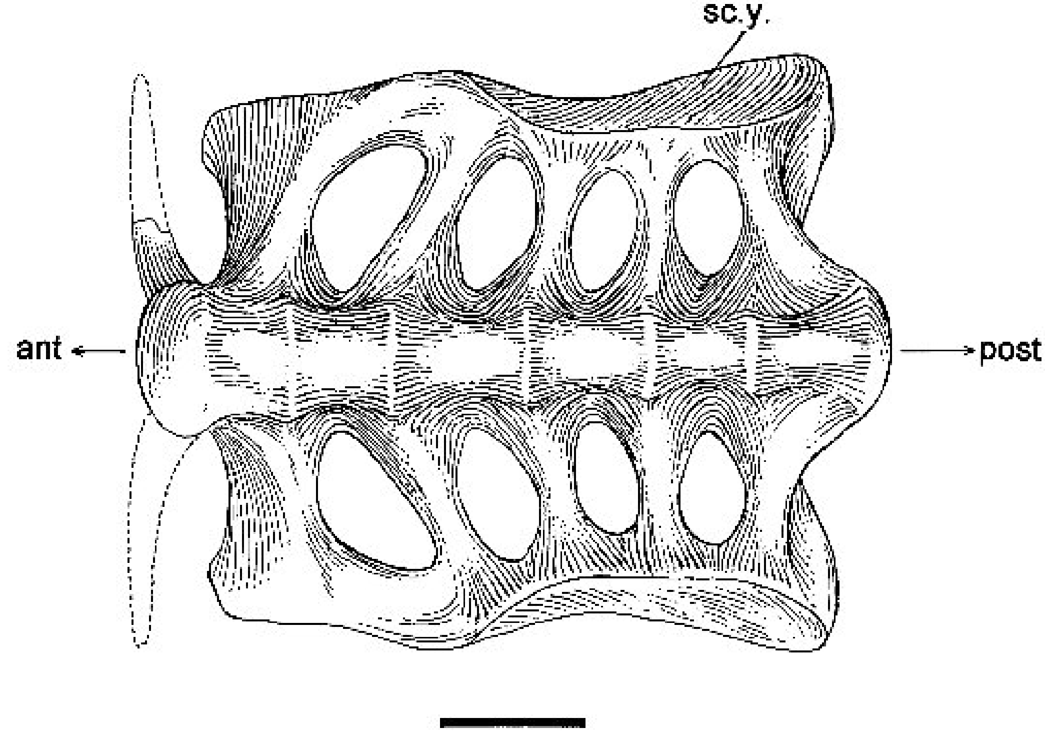

FIGURE 10. Ventral view of the sacrum of *T. colberti* (ISIR335/31). **Abbreviations: ant**, anterior; **post**, posterior; **sc. y.**, sacricostal yoke. Scale bar equals 20 cm.

imal end is rugose and roughly triangular with a strong anterior curvature. The olecranon process is inconspicuous. There is a marked depression on the lateral part of the proximal end. It is produced anteriorly into an angle with a deep concavity in the proximal part of the shaft for the reception of the head of the radius. A sharp ridge runs along the shaft of the ulna and merges into the distal end. The medial concavity is more prominent than the lateral one. The ulna shows a depression proximally on the shaft, while the rest of the shaft is flat. The middle of the shaft is triangular in cross section. The ulna gradually tapers towards the distal end, which is subovate in outline and smaller than the proximal end. Distally, the shaft has a marked depression, apparently for the reception of the distal end of the radius. The humerus/ulna length ratio is 25:14.

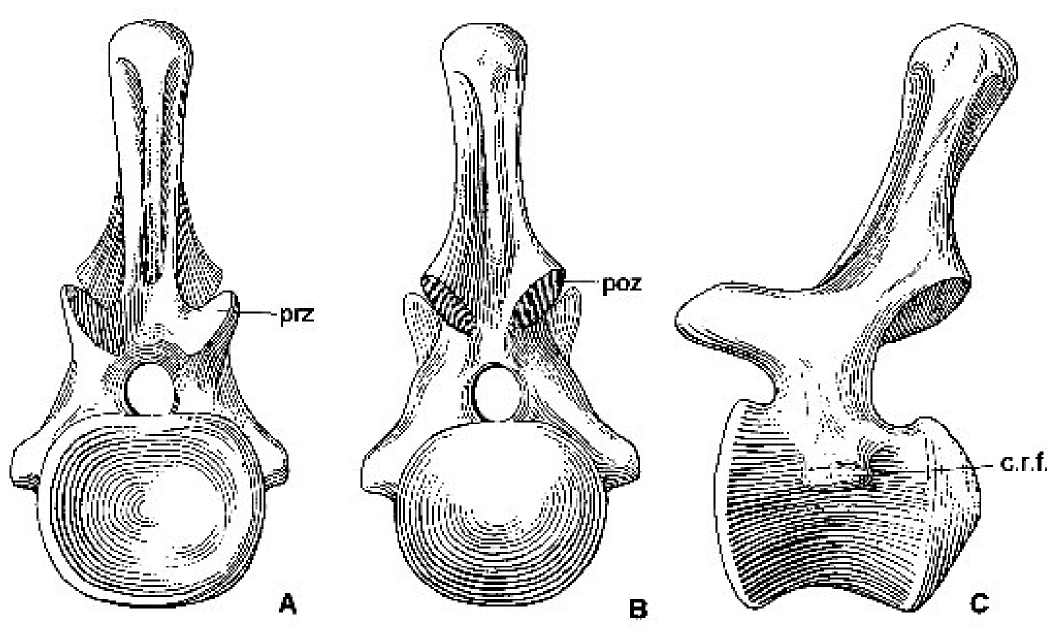

FIGURE 11. Proximal caudal vertebra of *T. colberti* (ISIR335/32) in, **A**, anterior; **B**; posterior; and **C**, lateral views. **Abbreviations: c.r.f.**, caudal rib facet; **poz**, postzygapophysis; **prz**, prezygapophysis. Scale bar equals 10 cm.

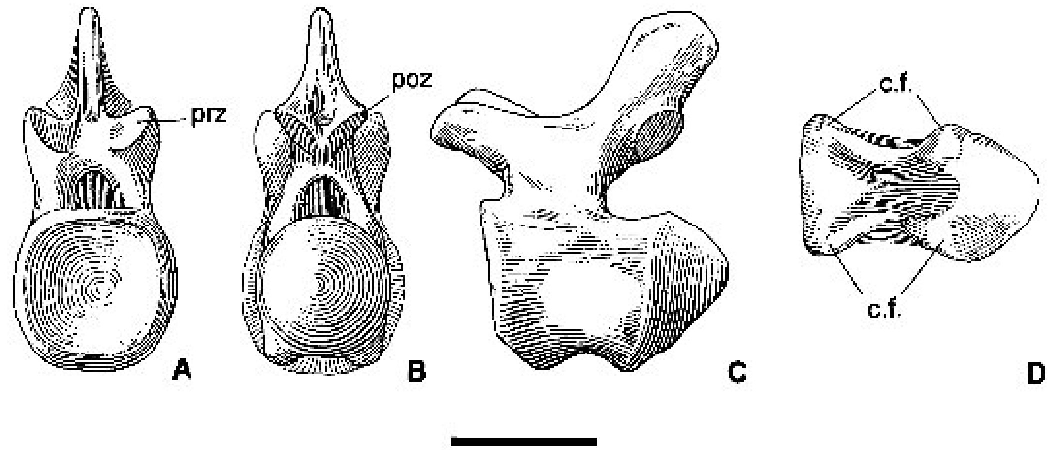

FIGURE 12. Midcaudal vertebra of *T. colberti* (ISIR335/42) in, **A**, anterior; **B**, posterior; **C**, lateral; and **D**, ventral views. **Abbreviations: c. f.**, chevron facet; **poz**, postzygapophysis; **prz**, prezygapophysis. Scale bar equals 10 cm.

Ulna measurements (in centimeters): length, 80; proximal transverse width, 36, distal transverse width, 21; minimum width of the shaft, 15.

Pelvic Girdle

All the pelvic bones, except the left ischium (which was not found) were found close to the sacrum. The left ilium (ISIR335/61) was found in direct articulation with the sacrum. The sacricostal yoke was found in a coossified state with the ilium. The right ilium (ISIR335/62) was found less than a meter away from the sacrum, but it could be articulated perfectly with the sacrum. It may be noted that whereas the left ilium was fully co-ossified and fused at the articulating surface with the sacrum, the right ilium was neither fused nor co-ossified. We are not aware of such a disparity between the left and right hand sides of an individual; as such we refrain from commenting on the implication of this condition. The right ischium (ISIR335/65) and left pubis (ISIR335/63) were found in overlapping position behind the sacrum. The right pubis (ISIR335/64) was also very close to the above (Fig. 2A).

Ilium (Figs. 21G, H, 23)—Both of the ilia are reasonably well preserved. With the exception of the anteriormost extremity of the iliac blade, the right ilium is complete.

The ilium has a long, curved preacetabular process, which is high and quite robust. It has an extensive lateral projection that almost forms a horizontal shelf. Ventrally, the preacetabular process has a deep oval depression that runs horizontally and bears parallel ridges indicating calcified tendons. Behind the actabular region, the bone flares laterally and continues up to the posterior end. This posterior flare is less robust than the preacetabular process having a posterior oval end. In the left ilium, a flared ridge running horizontally and internally along the iliac blade is co-ossified with the sacricostal yoke of the left side of the sacrum.

The acetabulum is very wide and high. It forms an embayment in the lower edge of the iliac blade and its surface is cup-shaped, bounded along the the upper edge by a rim. The inner surface of the acetabulum is highly rugose, marked by vertical ridges. Our restoration is largely based on the right ilium, but the anterior portion of the iliac blade has been reconstructed from the left side.

The pubic peduncle in both ilia is enlarged, robust, rugose, and has an subovate shape. The ischiadic peduncle of the right ilium is complete; in contrast to the pubic peduncle, the ischiadic peduncle is feeble.

Pubis (Figs. 21E, F, 24)—Both left and right pubes are preserved, although neither is complete. The iliac symphyseal region is intact in the left pubis (ISIR335/63), but the pubic basinal section and the ischial symphysial region are damaged. The right pubis (ISIR335/64) is twisted; nevertheless, the ischial symphyseal region is better preserved than on the left side; the iliac peduncle has been shifted towards the ischiadic pe-

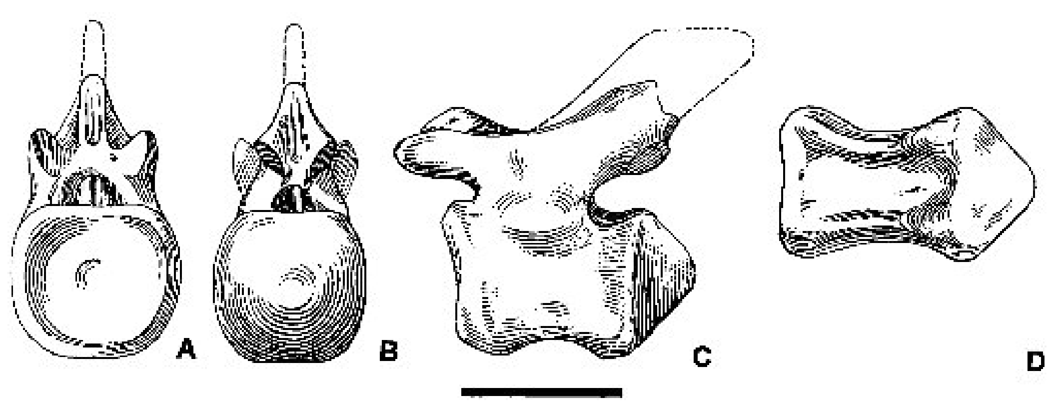

FIGURE 13. Distal caudal vertebra of *T. colberti* (ISIR335/44) in, **A**, anterior; **B**, posterior; **C**, lateral; and **D**, ventral views. Scale bar equals 10 cm.

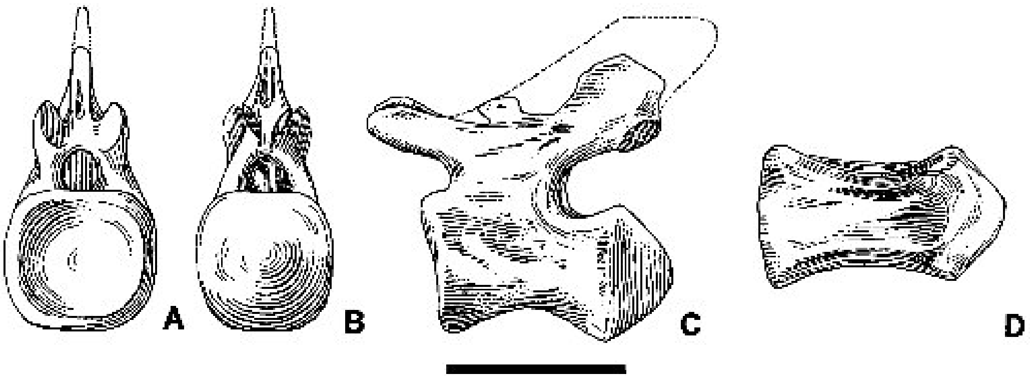

FIGURE 14. Distal caudal vertebra of *T. colberti* (ISIR335/46) in, **A**, anterior; **B**, posterior; **C**, lateral; and **D**, ventral views. Scale bar equals 10 cm.

duncle. The following description is based on both right and left pubes.

The pubis is stoutly built with expanded ends, especially proximally. It forms the anteroventral margin of the acetabulum. The acetabular embayment, which can be partly seen, is quite stout. The pubic foramen is somewhat damaged but appears to open downward immediately below the acetabulum. The iliac peduncle is well preserved, broad, and subovate in shape. The ischiadic symphyseal portion of the pubis is thin, extending almost to the midlength of the bone as seen in ISIR335/64. The shaft of the pubis is quite broad in the upper half of the bone, whereas it narrows ventrally but expands again slightly at the distal end. It is relatively thin along the posterior margin but quite stout along the anterior face. The distal end is rounded, and the symphyseal contact between the two pubes is well marked, swollen, and rugose. A strong ridge runs obliquely and anterolaterally along the shaft of the pubis up to the distal end. In addition, small ridge runs anteriorly alongside the main ridge. On either side of these ridges, there are marked depressions for muscle attachment area.

Measurements (in centimeters): right pubis (ISIR335/64); left pubis (ISIR335/63)—length, 84/100; maximum proximal width, 33/36; maximum distal width, 21/30; minimum width of the shaft, 22/20.

Ischium (Figs. 21I–J, 25)—The ischium (ISIR335/65) is flat and bladelike. The proximal end has a broadly expanded articulating surface for the peduncle of the ilium followed by a curved embayment with rugosities marking the acetabular part of the ischium. Anteriorly, another facet, which is quite thin, articulated with the pubis. Distally, the blade of the ischium is somewhat expanded and rugose. The conjoined ischia apparently articulated at the posterior end along the rugose, roughened surface. The shaft of the ischium is generally very thin, transversely elongated in the middle, and with a well marked rounded posterior border. The shaft is quite broad immediately below the acetabulum but becomes narrower ventral to the midpoint. The acetabular embayment of the ischium is rather smooth. Measurements of the ischium are: total length, 75 cm; maximum proximal width, 37 cm; maximum distal width, 26 cm; and minimum width of the shaft, 20 cm.

DISCUSSION AND COMMENTS

Titanosaurus Lydekker 1877, with *T. indicus* as the type species, was based upon two caudal vertebrae from Bara Simla Hill of Jabalpur (Jubbalpore), Central India. These vertebrae were "characterised by great lateral compression and by being markedly procoelous," thus producing flat-sided centra and a larger vertical diameter both on the anterior and posterior surfaces (Lydekker, 1879). Lydekker also noted "a pair of ridges which run from near the middle of the bone (centra) to the four angles of the inferior surface, in each case running from the center to the periphery of this surface"; and no postzygapophyses on the neural spine as well as no distinct articular facets on the prezygapophyses. He considered these vertebrae to be "the post-median moity of the caudal." Later, Huene and Matley (1933) studied these vertebrae and considered them as "the 10th to 12th caudal."

Huene and Matley (1933) described additional material (two caudals, one chevron, left tibia and a right fibula) of *T. indicus*

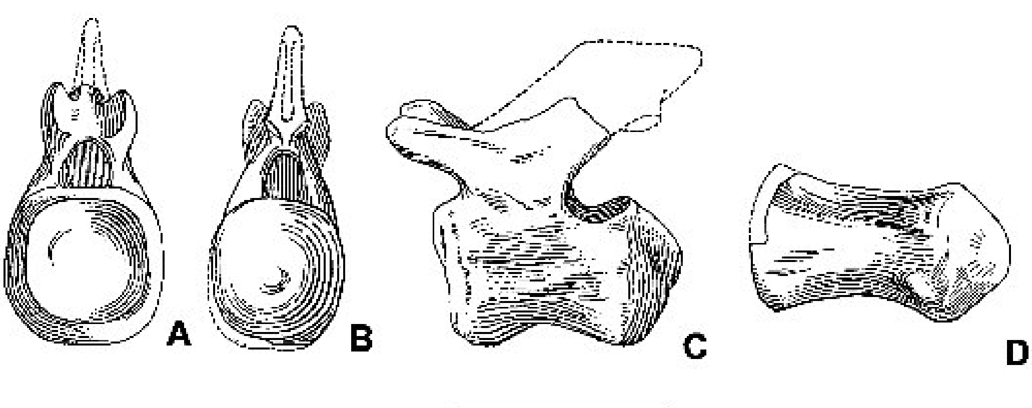

FIGURE 15. Distal caudal vertebra of *T. colberti* (ISIR335/47) in, **A**, anterior; **B**, posterior; and **C**, lateral views. Scale bar equals 10 cm.

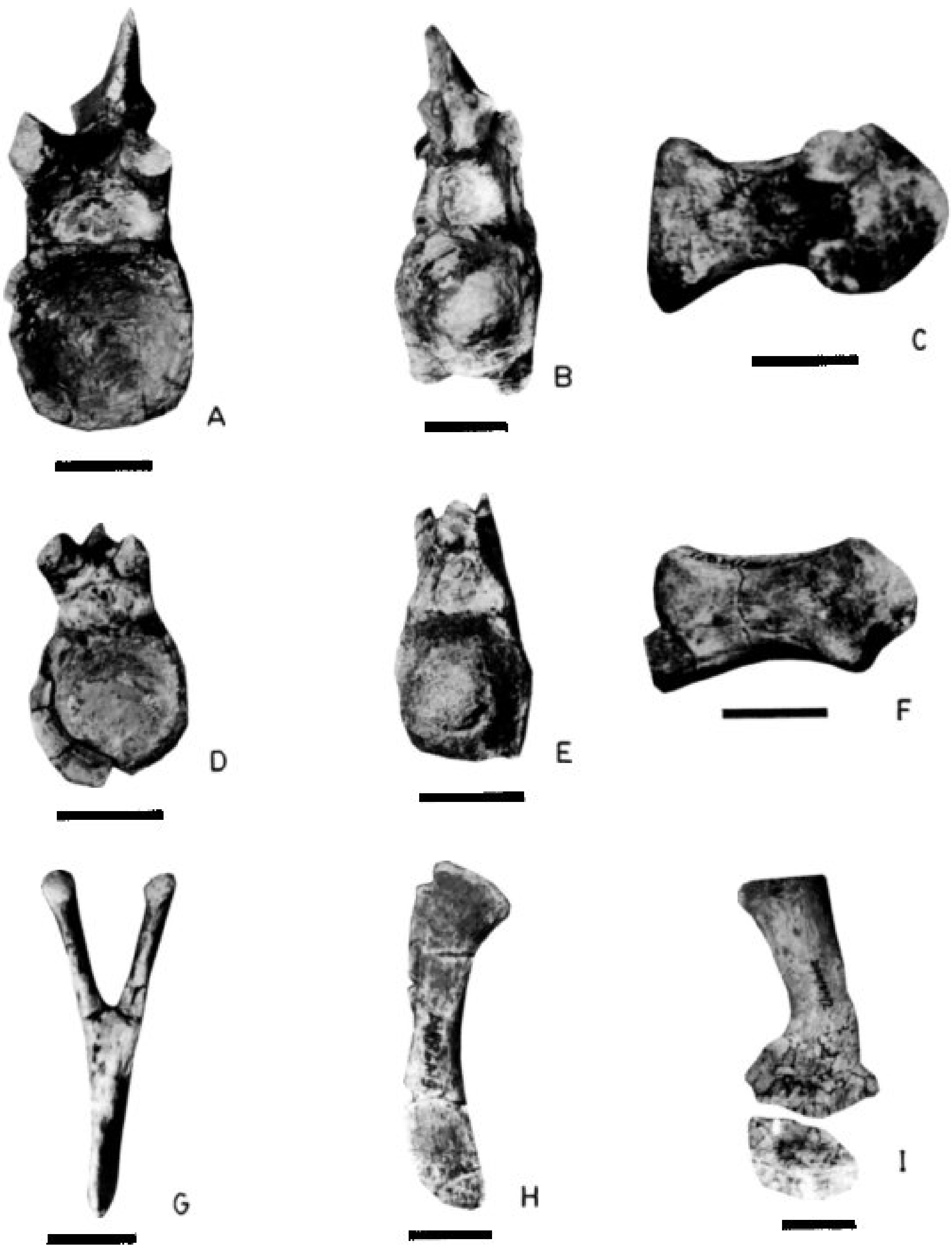

FIGURE 16. **A–C**, anterior, posterior and ventral views of a midcaudal vertebra (ISIR335/43). **D–F**, anterior, posterior and ventral views of a distal caudal vertebra (ISIR335/46). **G, H**, anterior and lateral views of a chevron bone (ISIR335/54). Scale bars equals 5 cm. **I**, lateral view of the scapula coracoid (ISIR335/57 and ISIR335/58). Scale bar equals 30 cm.

from the same region of Jabalpur. The two caudal vertebrae "were found together" along with the chevron. Huene and Matley (op. cit.) considered these caudals similar to the caudals of *T. indicus* described by Lydekker (op. cit.). There are, however, a few differences between Lydekker's and Huene and Matley's material. In the latter, one of the two caudals (K20/315) is procoelous, the other (K20/316) is amphicoelous. There is a "median, longitudinal groove between the two ridges" on the ventral surface of both caudals. A change from procoely to amphicoely is known to occur in some of the early sauropods including titanosaurids, eg., *Janenschia* (McIntosh, 1990a; Wild, 1991), *Andesaurus* (Calvo and Bonaparte, 1991) and *Malawisaurus* (Jacobs et al., 1993). Thus far there is no record of amphicoelous caudal vertebrae in any Maastrichtian titanosaurid. *Titanosaurus falloti* from the Late Cretaceous of Laos is known to have amphicoelous caudals (Hoffet, 1942), but McIntosh (1990a) pointed out that "it may belong to another genus and possibly another family." It is quite possible that the amphicoelous vertebra, K20/316, may not belong to a titanosaurid. Huene and Matley (1933) also described three midcaudals and a fragmentary sacral of *T. indicus* from Pisdura, another locality some 320 km south of Jabalpur (Fig. 1). The caudals are similar to those of the Jabalpur

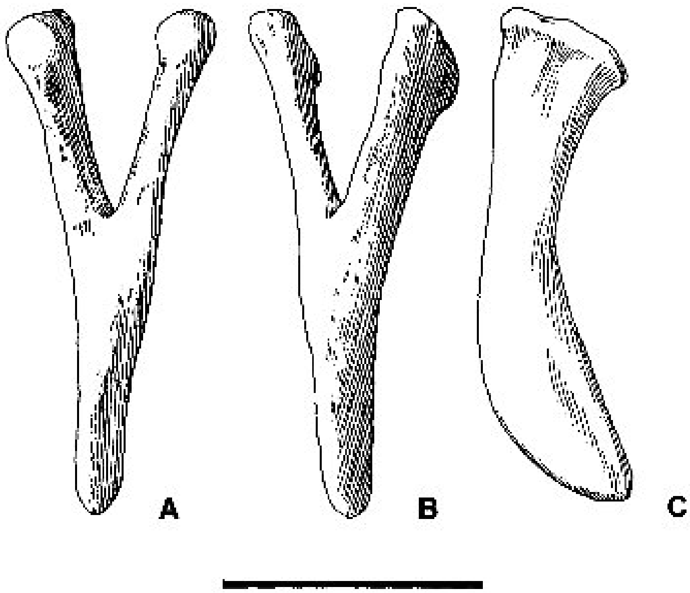

FIGURE 17. Chevron of *T. colberti* (ISIR335/54) in, **A**, anterior; **B**, posterior; and **C**, lateral views. Scale bar equals 10 cm.

TABLE 2. Comparative measurements of the scapulae (centimeters) of *Titanosaurus colberti* and *Antarctosaurus septentrionalis* from Bara Simla Hill, Jabalpur (Huene and Matley, 1933) and *Saltasaurus* sp. PVL-4017 - 106 (Powell, 1986).

	Titanosaurus colberti ISIR335/57	*Antarctosaurus septentrionalis*	*Saltasaurus* sp.
Total length of scapula	108	167	64
Maximum breadth of distal part	60	64.5	34
Minimum breadth of scapular blade	29	28	15
Maximum breadth of proximal part	43	—	—

material, although they are larger. However, the sacral is too fragmentary to permit a more precise determination.

Some titanosaurid limb bones that were associated with vertebrae and collected by C. A. Matley during 1917–1919 (Huene and Matley, 1933) from an adjacent locality of Bara Simla Hill of Jabalpur, known as Chota Simla hill, were not described at that time. The limb bones were later described by Swinton (1947) and identified as *T. indicus*, but the vertebrae were neither figured nor commented upon by Swinton. For this reason, we are also unable to comment upon these.

Prasad and Verma (1967) briefly described limb bones and vertebrae from the Lameta beds of Rajulwari village of Nagpur district, Maharashtra, assigning them to cf. *T. indicus* Lydekker. The vertebrae, although partly broken, have been determined as the 9th and 10th caudals by the authors. Though the photographs do not give adequate information about the material, we accept the vertebrae as caudals but the determination about their position is equivocal. The photograph of the assembled hind limb bones show no resemblance to any titanosaurid. *T. indicus* is also known from the Ariyalur beds of the Tiruchirapalli district of South India (Matley, 1929; Prasad, 1968) but no details of the material are available.

Lydekker (1877) did not provide a strict diagnosis of *Titanosaurus*. However, Huene and Matley (1933) provided a very general diagnosis of *Titanosaurus indicus*, which is valid for titanosaurids in general given the current status of our knowledge. A precise diagnosis of the genus *Titanosaurus* has not been published to date.

Another allied titanosaurid, described by Huene and Matley (1933) from Bara Simla Hill as *Antarctosaurus septentrionalis*, has been questioned by Weishampel (1990) and McIntosh (1990a). This titanosaurid was represented by an incomplete braincase, caudal vertebrae, chevron, ribs, scapulae, forelimbs, and probable sternal plates. Weishampel (1990) considered it as incertae sedis. Though McIntosh (1990a) questioned its generic identity, he considered it to be representative of a true

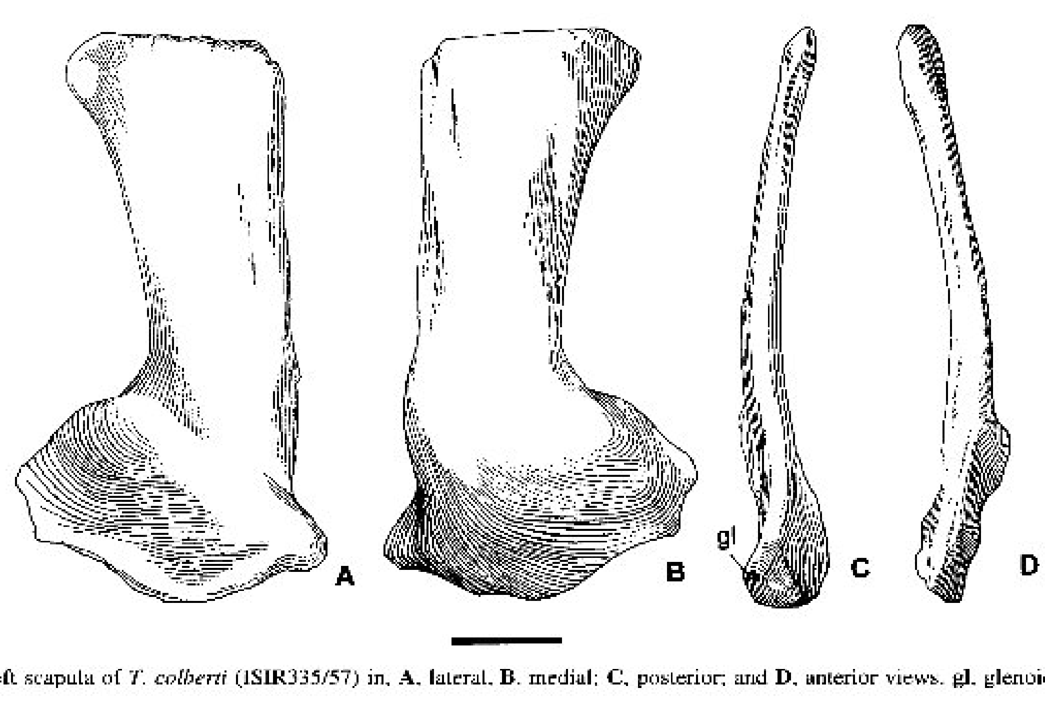

FIGURE 18. Left scapula of *T. colberti* (ISIR335/57) in, **A**, lateral, **B**, medial; **C**, posterior; and **D**, anterior views. **gl**, glenoid. Scale bar equals 20 cm.

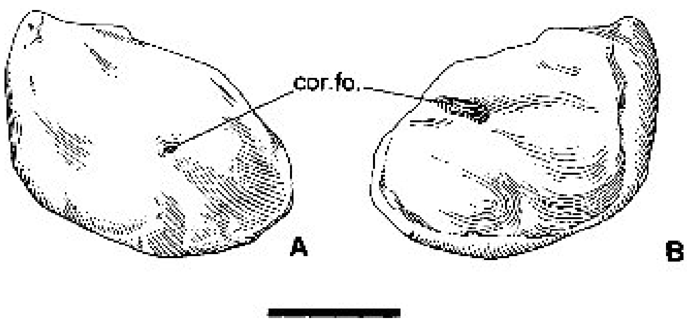

FIGURE 19. Left coracoid of *T. colberti* (ISIR335/58) in, **A**, lateral; and **B**, medial views. **cor. fo.**, coracoid foramen. Scale bar equals 20 cm.

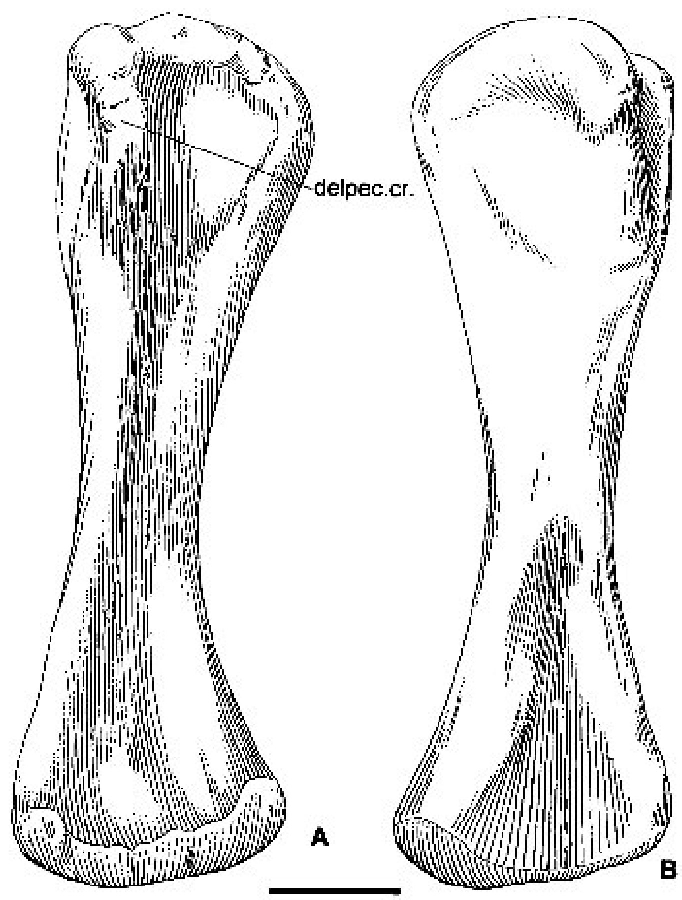

FIGURE 20. Left humerus of *T. colberti* (ISIR335/59) in, **A**, anterior; and **B**, posterior views. **delpec. cr.**, deltopectoral crest. Scale bar equals 20 cm.

titanosaurid. By comparing it with *Antarctosaurus wichmannianus* from South America, McIntosh found that the humerus does not resemble the latter, and the slender scapula of *A. septentrionalis* is relatively large and of a quite different shape. The large size of the bones along with the flat-sided caudal centra led him to consider it as a large titanosaur, but he did not assign it to any particular genus (McIntosh, 1990a:table 16.1). Jacobs et al., (1993), while describing new material of a titanosaurid (*Malawisaurus*) from the Early Cretaceous of Malawi, compared *Antarctosaurus* of South America with other titanosaurids, as well as diplodocids. They concluded that *Antarctosaurus* was originally mixed up with other sauropods and is possibly a diplodocid. Their conclusion was mainly based on the study of the maxillary region of the skull and the jaw structure. On this basis, they also doubted the generic identity of the Indian *Antarctosaurus*. Huene and Matley (1933) figured and described a left maxilla, K27/520, which they referred to the general level of Sauropoda. Jacobs et al., (1993) compared this material with other sauropod maxillae and concluded that it represented a titanosaurid. A comparison between the skeletal elements of *A. septentrionalis* and *T. indicus* indicates a very close similarity between the two forms, except for the larger size of the former. The caudals are procoelous and flat-sided in both forms. The enormously long scapula of *A. septentrionalis* (167 cm) is possibly due to the co-ossification of the suprascapula with the scapula. The slenderness of the scapula of *A. septentrionalis* is such that it is compatible with the slender limb bones of *T. indicus*. The humerus and the radius of the two are also very similar in shape and general characters. Swinton (1947), while describing the humerus of *T. indicus*, also mentioned that "the position and development of the radial process are thus in close agreement with the condition in *Antarctosaurus septentrionalis*." Both these forms were found from the Bara Simla Hill of Jabalpur. Because of the absence of any significant differences between these two forms, we believe *A. septentrionalis* is a junior synonym of *T. indicus*.

A second Indian species, *Titanosaurus blanfordi*, was described by Lydekker (1879) from Pisdura, central India. It is represented by two caudal vertebrae, one elongate the other short. Lydekker (1879) characterized the vertebrae as having nearly cylindrical centra without any lateral compression; the lateral surface clearly visible when viewed ventrally with no boundary between the lateral and the ventral surfaces; the transverse diameter of the articular surfaces longer than vertical diameter; and chevron facets that are not located on distinct ridges. However, we note that the short centrum does not strictly exhibit these characteristics. Huene and Matley (1933) referred this short vertebra to another species. Huene and Matley (1933) also described additional material of *T. blanfordi* from Pisdura. This included a caudal vertebrae, a tibia, a metacarpal, and a broken fragment of a probable scapula. It may be noted that the caudals show a close resemblance to Lydekker's short caudal of *T. blanfordi*, while the tibia and the metacarpal only show general sauropod features. In our opinion, only the elongated cylindrical vertebra should be referred to *T. blanfordi*. The short vertebra in Lydekker's description and Huene and Matley's material do not bear the typical characters of *T. blanfordi*.

Huene and Matley (1933) described a collection of one sacral and three caudals of similar length from Pisdura and assigned them to cf. *Laplatasaurus madagascariensis*. These caudals are short and thick with squarish articular surfaces. The ventral sides have a broad, flat groove and faint chevron facets. Deperet (1896) had previously described part of a humerus, two caudal vertebrae, and a dermal scute from the Late Cretaceous of Madagascar as *Titanosaurus madagascariensis*. Later, Huene (1929) changed the name to *Laplatasaurus madagascariensis*. However, both McIntosh (1990a) and Weishampel (1990) preferred to retain the original name, *T. madagascariensis*, although Weishampel questioned its taxonomy. The material from Pisdura that Huene and Matley (1933) referred to *Laplatasaurus madagascariensis* was referred to *T. madagascariensis* by McIntosh (1990a: table 16.1), a view shared by the present authors.

Huene and Matley (1933) changed the assignment of the short caudal of Lydekker's "*T. blanfordi*" to cf. "*Laplatasaurus*" *madagascariensis*. This should now be considered as *T. madagascariensis*. Similarly, the material described from Pisdura by Huene and Matley (1993) as *T. blanfordi* should also be considered as *T. madagascariensis*. Consequently, *T. blan-*

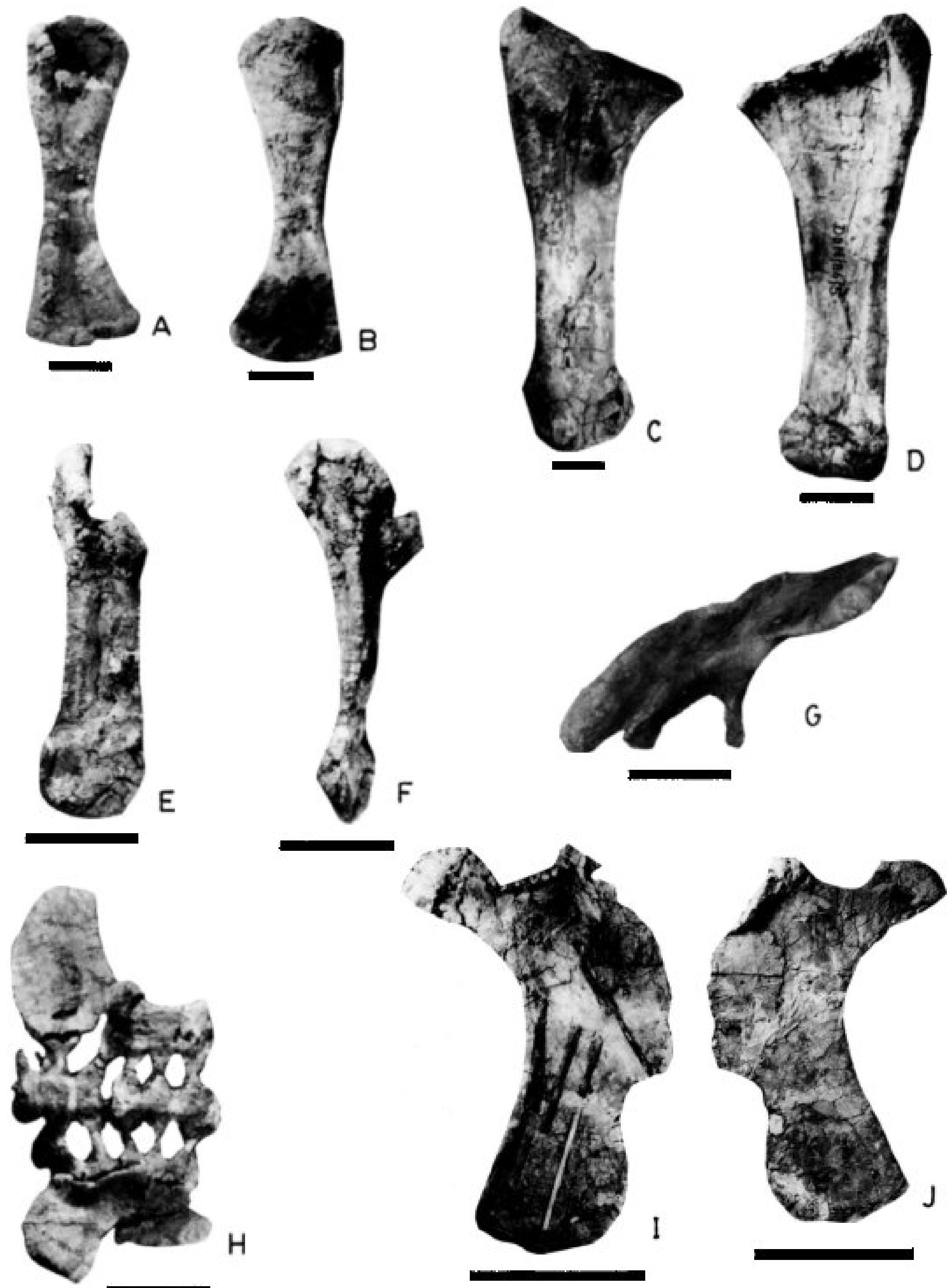

FIGURE 21. **A**, **B**, anterior and posterior views of the left humerus (ISIR335/59). Scale bar equals 25 cm. **C**, **D**, anterior and posterior views of the left ulna (ISIR335/60). Scale bar equals 10 cm. **E**, **F**, dorsal and lateral views of e left pubis (ISIR335/63). **G**, lateral view of the right ilium (ISIR335/62). Scale bars equal 30 cm. **H**, ventral view of the sacrum (ISIR335/31) with left and right ilia (ISIR335/61, ISIR335/62). Scale bar equals 50 cm. **I**, **J**, dorsomedial and ventrolateral views of the right ischium (ISIR335/65). Scale bars equal 30 cm.

fordi is based on but a single caudal vertebra that has an elongated, cylindrical centrum.

In summary, it may be seen that the diagnoses of *T. indicus*, *T. blanfordi*, and *T. madagascariensis* rest mainly on the shape of the midcaudal centra (flat-sided, cylindrical, or squarish), the comparative diameter of the articular surfaces of the centra, and the position of the chevron facets.

When compared with the three Indian titanosaurids, *Titanosaurus colberti* shows several differences. Comparison of the holotype material is naturally limited to the caudal vertebrae. The centra of the midcaudal vertebrae of *T. colberti* (Fig. 12), besides being strongly procoelous, are a little waisted in the middle, which results in slightly curved lateral and ventral surfaces. In addition, part of the lateral surfaces are visible when

TABLE 3. Comparative measurements of the humerii (centimeters) of *Titanosaurus colberti*, *Antarctosaurus septentrionalis* (Huene and Matley, 1933), *Titanosaurus indicus* (Huene and Matley, 1933 cf. Swinton, 1947), and the Pisdura titanosaur of the ISI collection.

	Titanosaurus colberti ISIR335/59	*Antarctosaurus septentrionalis*	*Titanosaurus indicus* R5931	Pisdura titanosaur (new collection)
Total length of humerus	148	134	93.1	80
Maximum breadth at proximal end	46	58	36.8	35
Maximum breadth at distal end	45	—	22.8	28
Minimum transverse width	21	23	11	15
Ratio of maximum length of scapula and humerus	148/108	—	—	—

viewed in ventral aspect. While the anterior articulating surfaces are well rounded, the posterior articulating surfaces are somewhat rectangular due to the presence of chevron facets. The vertical and transverse diameters are approximately equal, both on the anterior and posterior surfaces. Ventrally, the chevron facets are situated on very low faint ridges on the anterior rim, but posteriorly these facets are located on prominent high ridges. These ridges are incipient in the middle part of the ventral surface, which is waisted but flat. There is no suggestion of any cross ridges on the ventral surface as seen in *T. indicus* (Lydekker, 1879: pl. IV, fig. 1), nor any longitudinal median groove (Fig 26; Huene and Matley, 1933:fig. 2). There are well-developed neural arches with prominent prezygapophyses, which is consistent with the distinct articular facets on the postzygapophyses. Hence, the features of the midcaudal vertebrae of *T. colberti* are unique and differ from other Indian titanosaurids. Among other bones, the scapula, humerus, and ulna are known for *T. colberti* and *T. indicus*. The length of the scapula of the large *T. indicus* (i.e., "*Antarctosaurus septentrionalis*") is about one and a half times that of *T. colberti*. The maximum width of the scapula is marginally more in the latter, and it has a different shape altogether (Fig. 18, Table 4). It is essentially broad and squat by comparison with the slender scapula of *T. indicus*. The humerus of *T. colberti* is not only more than one and half times longer than *T. indicus* as described by Swinton (1947) but also more massively built. The proximal and the distal ends of the *T. colberti* humerus are more expanded (Table 3). In addition, the ulna of the large *T. indicus* described by Huene and Matley (1933) has a "somewhat rectangular" cross section, contrasting with the triangular shape of the shaft of the ulna in *T. colberti*. However, the identity of the ulna in the former was doubted by Huene and Matley. Thus, apart from the differences in the characteristic features of the midcaudal vertebrae, *T. colberti* also differs from *T. indicus* with respect to the appendicular elements. Comparable appendicular elements for *T. blanfordi* and *T. madagascariensis* are not available.

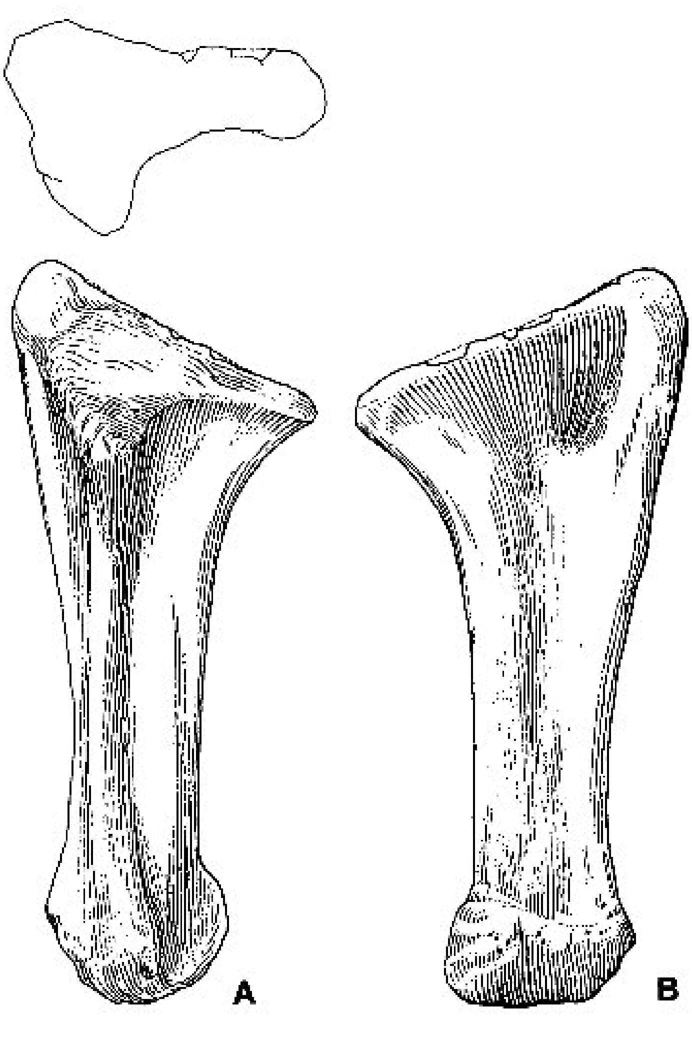

FIGURE 22. Left ulna of *T. colberti* (ISIR335/60) in, **A**, anterior; and **B**, posterior view. Scale bar equals 25 cm.

Titanosaurus indicus is also reported from other continents. Numerous caudal vertebrae, limb bones, four scapulae, and three pubes from Maastrichtian beds of central France have been reported by Lapparent (1947). Recently some material of *T. indicus* was also reported from Spain (McIntosh, 1990a) and *T. madagascariensis* is known from Madagascar (Deperet, 1896). Another species, *T. falloti*, was reported from Laos (Hoffet, 1942) and is represented by amphicoelous centra and a robust femur. Its validity has been questioned by McIntosh (1990a), and it should be noted that amphicoelous vertebrae are not found in the Late Cretaceous titanosaurids.

Mathur and Srivatsava (1987) described some isolated teeth from the Lameta beds of the Kheda district of Gujarat and doubtfully referred to them as *T. rahiolensis*. However, skull material and teeth of titanosaurids are extremely rare, and they are therefore of extremely limited value at present in the determination of titanosaurid species. As such, we consider ?*T. rahiolensis* to be indeterminate beyond the general level of sauropod. Mohabey and Udhoji (1990) and Mohabey et al. (1993) reported the presence of *Titanosaurus* sp. and *Antarctosaurus* sp. from the Late Cretaceous Lameta beds of the Nand and Pavna areas of Nagpur district and also of Dongargaon, Maharashtra. However, no details of the bones were given. References to fragmentary material from India assigned to titanosaurids have been questioned by Weishampel (1990) and McIntosh (1990a). In most cases, these have been considered as indeterminate, and we therefore will not comment on them further.

Chatterjee and Rudra (in press) commented on various as-

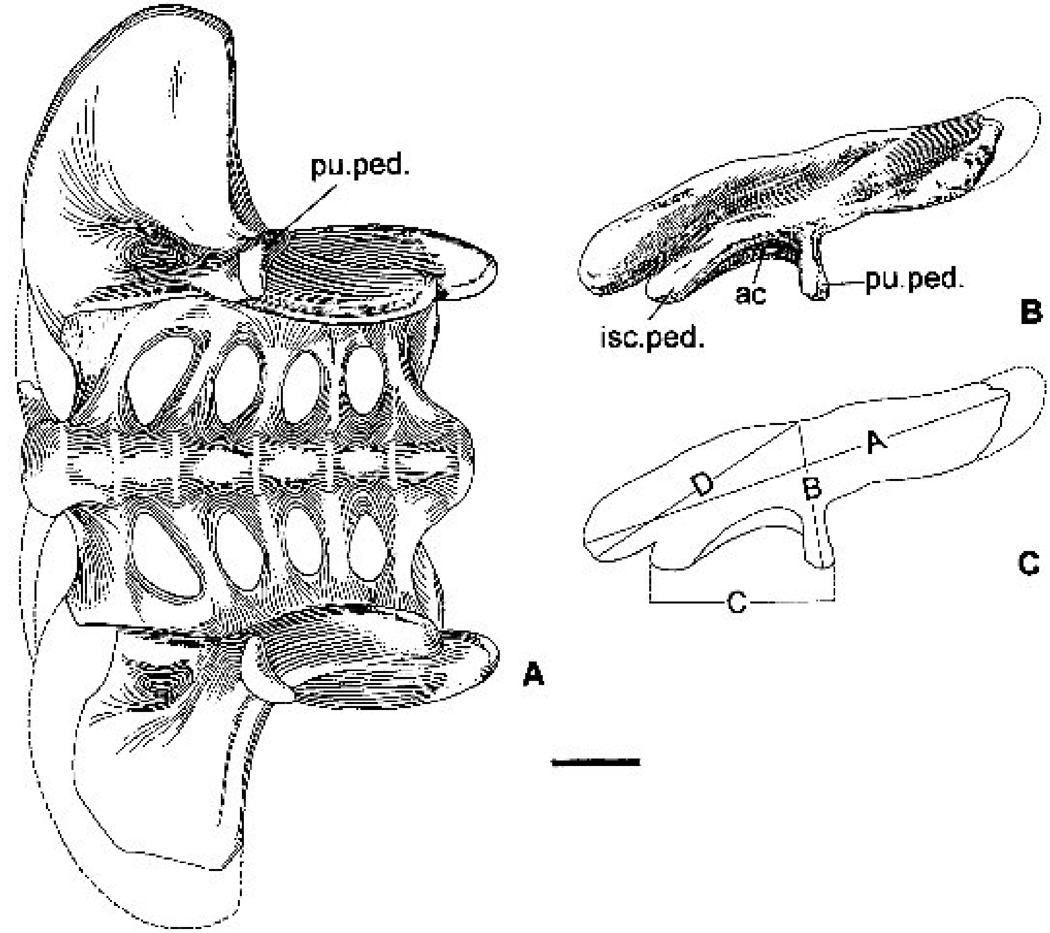

FIGURE 23. **A**, ventral view of the sacrum (ISIR335/31) together with both ilia (ISIR335/61 and ISIR335/62 respectively). **B**, lateral view of the right ilium (ISIR335/62) with the restoration of the iliac blade based on ISIR335/61. **Abbreviations: ac.**, acetabulum; **isc. ped.**, ischiadic peduncle; **pu. ped.**, pubic peduncle. Scale bar equals 20 cm. **C**, Outline sketch of the right ilium. The parameters measured are as follows: A, 80 cm; B, 50 cm; C, 40 cm and D, 60 cm.

pects of titanosaur taxonomy. They concluded that "there is no indication that more than one titanosaurid species is present in India." In addition to *T. colberti* (as discussed above), we consider *T. indicus*, *T. blanfordi*, and *T. madagascariensis* as valid species based on detailed morphological comparisons. Chatterjee and Rudra also comment on a statement by Jain (1989) that titanosaurid vertebrae collected as surface finds from the Dongargaon locality resemble *T. indicus*. Our present view based on extensive excavation of the site and examination of the material from Dongargaon, has led to conclude that all this material belongs to *T. colberti*. Chatterjee and Rudra (in press) also described new titanosaurid braincase material from Jabalpur. This site earlier yielded a braincase that was assigned to "*Antarctosaurus septentrionalis*" (Huene and Matley, 1933). Chatterjee and Rudra considered the two braincases to be very similar. Unfortunately, the braincase described by Huene and Matley (1933) has been lost (Berman and Jain, 1982), and the braincase described by Chatterjee and Rudra (in press) was not available to us. Nevertheless, a critical examination of the illustrations reveals differences in certain key features. Chatterjee and Rudra (in press) assign such differences to sexual dimorphism and are inclined to consider both braincases as *T. indicus*. The braincase from Dongargaon was compared with Huene and Matley's (1933) material by Berman and Jain (1982). The authors recognized considerable differences between the two, despite a few points of resemblance but refrained from assigning the Dongargaon material to any taxa beyond the general level of a titanosaurid. We agree with Chatterjee and Rudra (in press) in considering the braincase of "*A. septentrionalis*" as *T. indicus*. This is further supported by evaluation of other fossil material assigned to it and discussed by us earlier.

After the early discoveries of titanosaurids in India and South America, largely through the efforts of Lydekker (1877, 1879, 1893), Seeley (1888), Matley (1921), and others, Huene (1929) reviewed and consolidated the knowledge of titanosaurids at that time. Several reports of titanosaurid material from different parts of the world have since been published, but the taxonomy of the Titanosauridae has never been adequately treated. Romer (1956), in his classification of the Reptilia, retained thirteen genera of titanosaurids within the family Titanosauridae and subfamily Titanosaurinae. Later, Romer (1966) assigned eighteen genera to the family Titanosauridae, although some of the earlier designated taxa were shifted to other families. Steel (1970) considered fifteen titanosaurid genera within the family Atlantosauridae and subfamily Titanosaurinae (Table 4A). During the last two decades, an effort has been made by several authors to improve titanosaurid taxonomy and to identify key characters (Bonaparte and Powell, 1980; Powell, 1986, 1992; Gauthier 1986; Carroll, 1988; McIntosh, 1990a, b; Weishampel, 1990; Wild, 1991; Jacobs et al., 1993; Bonaparte and Coria, 1993). Several sauropod genera that have been referred to as titanosaurids still need clarification, and the validity of many

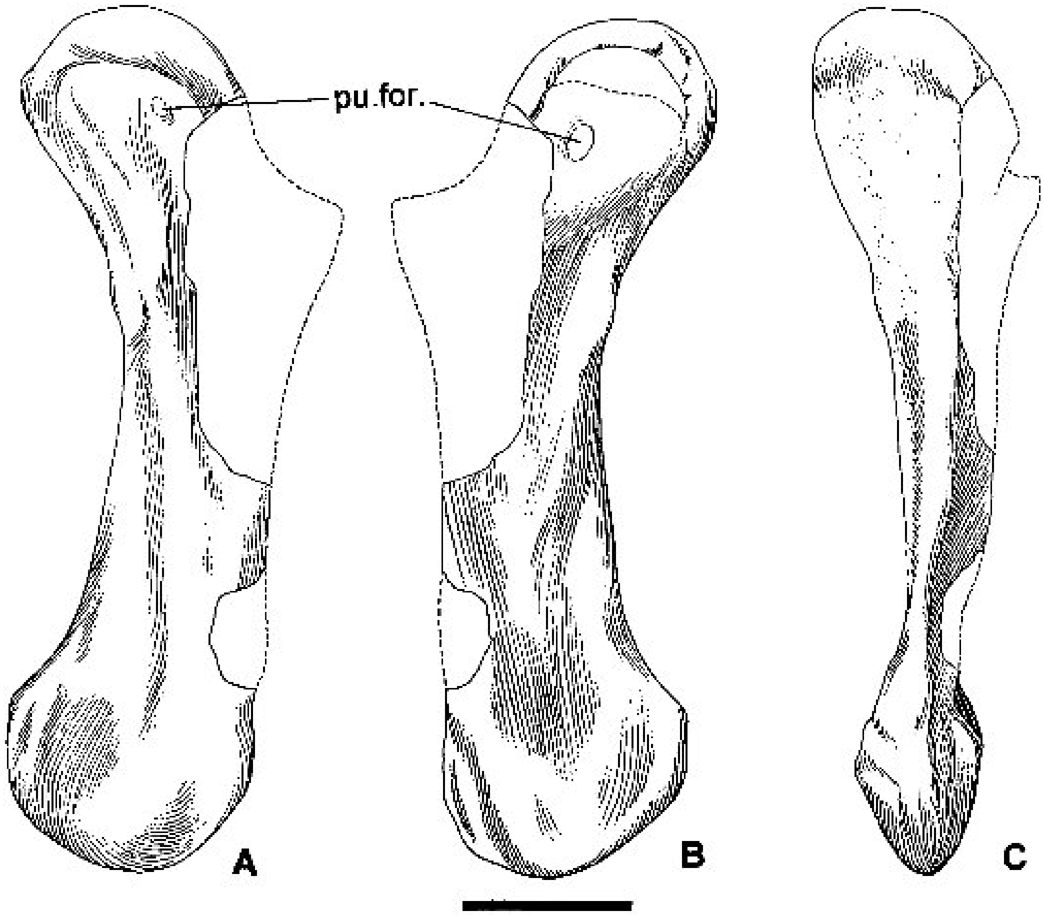

FIGURE 24. Left pubis of *T. colberti* (ISIR335/63) in, **A**, dorsal; **B**, medial; and **C**, lateral views. **pu. for.**, position of pubic foramen. Scale bar equals 10 cm.

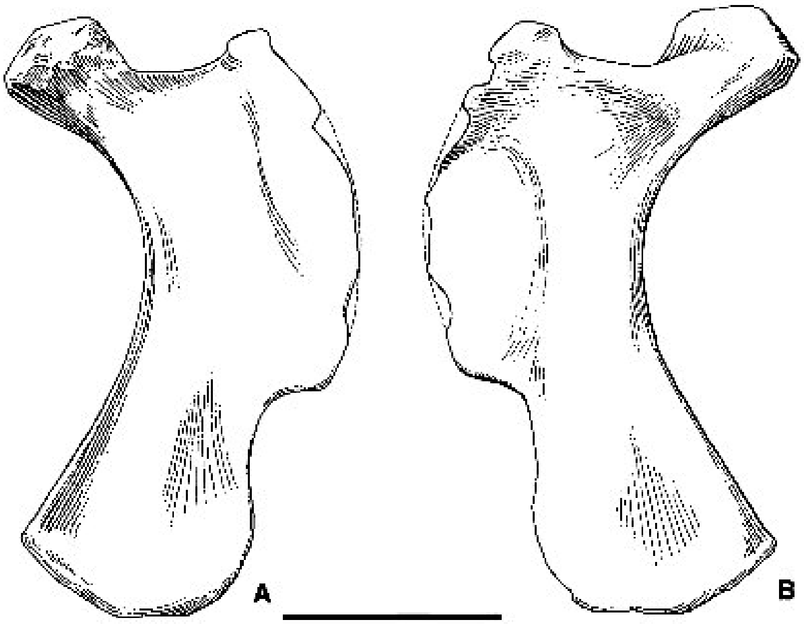

FIGURE 25. Right ischium of *T. colberti* (ISIR335/65) in **A**, dorsomedial; and **B**, ventrolateral views. Scale bar equals 25 cm.

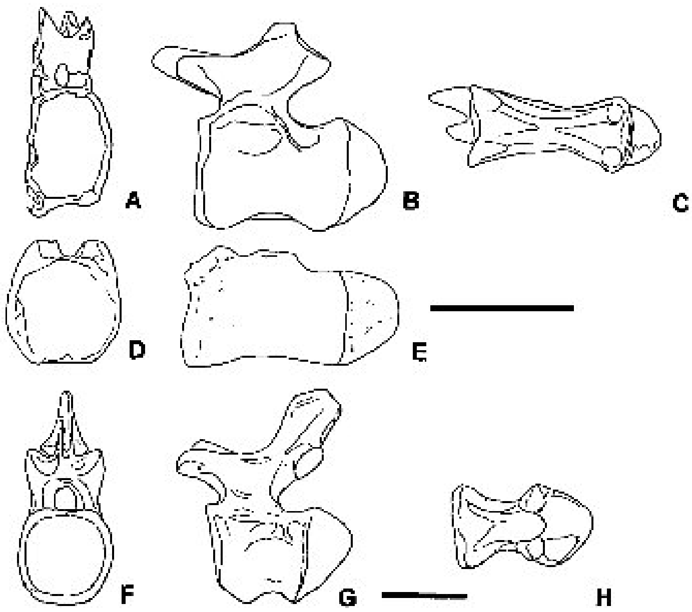

FIGURE 26. Views of the midcaudals of A–C, *Titanosaurus indicus* Lydekker 1877 (**A**, anterior; **B**, lateral; and **C**, ventral views). **D**, **E**, *Titanosaurus blanfordi* Lydekker 1877 (**D**, Anterior; and **E**, lateral views). **F**–**H**, *Titanosaurus colberti* (**F**, Anterior; **G**, lateral; and **H**, ventral views). Scale bars equal 10cm.

titanosaurid genera is questionable because of the incompleteness of the material.

Powell (1986) recognized the taxonomy of some South American titanosaurid genera by subdividing the family Titanosauridae into four subfamilies—Titanosaurinae Lydekker, 1893; Saltasaurinae, nov.; Antarctosaurinae, nov.; and Argyrosaurinae, nov. (Table 4B). In addition, he changed the status of some of the earlier described titanosaurid genera. He transferred part of *Titanosaurus australis* and *T. robustus*, both Argentinian titanosaurids, to *Neuquensaurus australis* and *N. robustus*, respectively. He also synonymized *Laplatasaurus araukanicus* with *Titanosaurus araukanicus* and changed part of *T. australis* and *T. robustus* to *T. araukanicus*. Gauthier (1986), while giving a detailed analysis of sauropod monophyly, divided the Sauropoda into two principal groups—titanosaurs and camarasaurs. He further subdivided the titanosaurs into "two informal taxa"—antarctosaurs and diplodocids, with the antarctosaurs, including *Antarctosaurus*, *Alamosaurus*, *Laplatasaurus*, and *Titanosaurus*, characterized by a caudal series with a biconvex first caudal centrum followed subsequently by procoelous caudals. Carroll (1988) provided a world-wide list of fifteen titanosaurid genera within the family Titanosauridae Lydekker, 1885 (Table 4C), and without the fourfold division of the family as proposed by Powell (1986). McIntosh (1990a) maintained this system except for changing a few genera (Table 4D). McIntosh (1990a), however, did not follow Powell's suggestion (1986) and considered *T. australis* and *T. robustus* as *Saltasaurus australis* and *S. robustus*, respectively. He also retained *Laplatasaurus araukanicus*. McIntosh (1990a, b) further commented that in most cases due to a lack of skull material the relationship of titanosaurid with other sauropod families is not clear. Calvo and Bonaparte (1991) described a new species *Andesaurus delagadoi* and erected a new subfamily Andesaurinae within the family Titanosauridae (sensu Powell, 1986). Recently, Bonaparte and Coria (1993) raised the subfamily Andesaurinae to the family level and included three South American titanosaurid genera, *Argentinosaurus*, *Andesaurus*, and *Epacthosaurus*. All these titanosaurid genera share the presence of a hyposphene and hypantrum.

Some of the earlier titanosaurid finds from North Africa have been recently reevaluated. *Tornieria*, represented by *T. africanus* and *T. robusta*, was described by Sternfield (1911) from the Tendaguru beds of Tanzania. Later, *T. africanus* was reassigned to *Barosaurus africanus* by Janensch (1922). Similarly, *T. robusta* was changed to *Janenschia robusta* by Wild (1991). Jacobs et al. (1993), while describing *Malawisaurus dixey* from Malawi, North Africa, included *T. dixey* in this new taxon.

It may be noted that South America has the largest number of titanosaurid genera (11) followed by Europe (5), Africa (3), and then North America, Asia, Madagascar and India (each with 1) (Table 5). At present, the associated and articulated skeletons of individuals of *Saltasaurus loricatus* provide the most nearly complete information about the skeletal elements of any titanosaurid. It was collected from the Lecho Formation of the Salta Group of Argentina and is Late Cretaceous (Senomanian-Maastrichtian) in age (Bonaparte and Powell, 1980; Powell, 1986, 1992). It is a medium-sized, stocky limbed animal. *Saltasaurus* differs from *T. colberti* in its estimated size, with *T. colberti* probably twice the size of *Saltasaurus*. The ischium of *T. colberti* is more transversely expanded than in *Saltasaurus*, and the shape of the ilium is also very different. Moreover, the sacrum of *T. colberti* has a rather different articulation with ilium. The other Late Cretaceous titanosaurids are either incompletely known or the known skeletal elements are absent in *T. colberti*. The scapula of *Alamosaurus* from North America is not only large, but proximally it also maintains a

TABLE 4. Taxonomic status of titanosaurid genera as proposed by (A) Steel (1970), (B) Powell (1986), (C) Carroll (1988), and (D) McIntosh (1990a).

A Family Atlantosauridae Marsh, 1877 Subfamily Titanosaurinae Nopsca, 1928	B Family Titanosauridae Lydekker, 1893	C Family Titanosauridae	D Family Titanosauridae Lydekker, 1885
Aegyptosaurus, Aepisaurus, Alamosaurus, Algosaurus, Antarctosaurus, Apatodon, Argyrosaurus, Campylodoniscus, Hypselosaurus, Laplatasaurus, Macrurosaurus, Parrosaurus, Succinodon, Titanosaurus, Tornieria	Subfamily Titanosaurinae Lydekker 1893 *Titanosaurus, Aeolosaurus* Subfamily Saltasaurinae, nov. *Saltasaurus, Neuquensaurus, Microcoelus* Subfamily Antarctosaurinae nov. *Antarctosaurus* Subfamily Argyrosaurinae nov. *Argyrosaurus, Epacthosaurus, Clasmodosaurus*	*Aegyptosaurus, ?Aepisaurus, Alamosaurus, ?Algosaurus, Antarctosaurus, Argyrosaurus, Campylodoniscus, Chubitosaurus, Hypselosaurus, Laplatasaurus, Loricosaurus, ?Macrurosaurus, Saltasaurus, Titanosaurus, (Magyasaurus), Tornieria*	*Titanosaurus, Magyasaurus, Laplatasaurus, Saltasaurus, Aegyptosaurus, Alamosaurus, Macrurosaurus, Argyrosaurus, Hypselosaurus, Antarctosaurus, Tornieria*

TABLE 5. Distribution of titanosaurid genera (after Powell, 1986; Carroll, 1988; McIntosh, 1990a; Jacobs et al., 1993; Bonaparte and Coria, 1993).

Age	Region	North America	South America	Africa: North Africa	Africa: East Africa	Europe	Asia/India	Madagascar
CRETACEOUS	Upper	*Alamosaurus*	*Antarctosaurus*	*Aegyptosaurus*		*Hypselosaurus*	*Titanosaurus*	*Titanosaurus*
			Aeolosaurus			*Macrurosaurus*		
			Argentinosaurus			*Magyarosaurus*		
			Andesaurus			*Titanosaurus*		
			Clasmodosaurus			*Succinodon*		
			Epachthosaurus					
			Laplatasaurus					
			Microcoelus					
			Saltasaurus					
			Titanosaurus					
	Lower				*Janenschia*			
					Malawisaurus			

large angle between the shaft and the ridge. This feature is not seen in *T. colberti*.

L. I. Price collected unique skeletal elements of a titanosaur from the Marilia Formation of the Upper Bauru Group of Brazil (Maastrichtian-Campanian) (Bertini et al., 1991). This material has remained undescribed for several decades. Some photographs and line drawings of this skeletal material were made available to us through the courtesy of the late Dr. Pamela L. Robinson. McIntosh (1990a) has also figured some of this undescribed material. Some of the skeletal elements are apparently similar to *T. colberti*. The first sacral rib (i.e., the rib of the second dorsosacral) of *T. colberti* projects laterally and extends to the ilium. The photographic material at our disposal suggests that such a relationship exists in the undescribed material from Brazil in which the first sacral rib is extended below the iliac blade and fused with it. However, the Brazilian form has an isolated biconvex vertebra (probably the first caudal) and a very slender ischium with a rather curved ischial symphysis. *T. colberti* does not have a biconvex first caudal centrum, and its ischia are transversely expanded and the symphiseal region is straight.

T. colberti is a distinct titanosaurid when compared with all other titanosaurids. The Early Cretaceous titanosaurids *Janenschia* and *Malawisaurus* have procoelous proximal caudal vertebrae but in the midcaudal series, the vertebrae become amphicoelous, whereas *T. colberti* has strongly procoelous caudal vertebrae throughout the caudal series. *T. colberti* is a medium-sized advanced titanosaurid represented by a single individual, which enables us to better understand the characteristics of *Titanosaurus*. We give below a revised diagnosis of the genus *Titanosaurus*. Other synonyms have been extensively covered by Steel (1970), Powell (1986), McIntosh (1990a), Weishampel (1990), and Bonaparte and Coria (1993), and will not be commented upon here. However, we would like to point out that the biconvex feature of the first caudal centrum has been regarded as one of the features of several titanosaur taxa (Gauthier 1986). This feature is exhibited in *Alamosaurus sanjuanensis* (Gilmore, 1922, 1946; Mateer, 1976) and *Titanosaurus australis* (Huene, 1929), and the undescribed titanosaur from the Bauru Formation of Brazil. Hence we do not include this feature in our diagnosis.

Genus TITANOSAURUS Lydekker, 1877

Revised Diagnosis—Large advanced sauropods with strongly procoelous caudals throughout the series; cervicals and dorsals opisthocoelous with well-marked pleurocoels; transverse process of cervicals robust, directed laterally, very wide posteriorly in shoulder region; transverse process in dorsals narrow and directed outward and a little upward; neural spine not bifid, directed posteriorly; sacrum with six co-ossified vertebrae and ribs; first and sixth sacral centra convex anteriorly and posteriorly respectively; midcaudal and part of distal caudals with prominent variable chevron facets; robust prezygapophyses extending to the anterior margin of the caudals; first sacral rib extended outward below the iliac blade; preacetabular process of the ilium projecting outward becoming almost horizontal; bladelike ischium transversely expanded in the middle; shaft of slender radius perpendicular to the axis of the expanded distal ends; ulna robust and triangular in cross section; humero-femoral ratio 0.74; tibio-femoral ratio 0.65; femur without any lateral prominence; moderate development of nuchal crest of braincase; transverse ridge on parietal, high buttress ridge below the paroccipital process.

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