The Middle Jurassic Dinosaurian Fauna from Dashanpu, Zigong, Sichuan

Vol. I

The Ornithopod Dinosaurs

by

Xinlu He and Kaiji Cai

(Laboratory of Vertebrate Paleontology, Chengdu College of Geology)

Sichuan Scientific and Technological Publishing House
September, 1984

Provided by support from The Dinosaur Society

Translated by Will Downs
Bilby Research Center
Northern Arizona University

Introduction

In 1973, an ornithischian skeleton was discovered in Late Jurassic sediments at the Jinzidang composter, near Hongheba Dam, southeast of Zigong municipality, Sichuan Province. Subsequently, in 1979, Xinlu He conducted a brief description and erected the name *Yandusaurus*[*] *hongheensis.* Later, in 1981, more abundant ornithischian remains were discovered in Middle Jurassic deposits northeast of Zigong at the town of Dashanpu. These were published in a short 1983 report by He and Kaiji Cai, who erected the name *Yandusaurus multidens.* The relatively well preserved and abundant material of this latter taxon now shows the previously rare Hypsilophodontidae to be abundantly represented. This paper is intended as a detailed description and discussion of the Dashanpu ornithischians in addition to a supplementary description of the Hongheba material. Finally, taxonomic comparisons with related forms outside of China will be made.

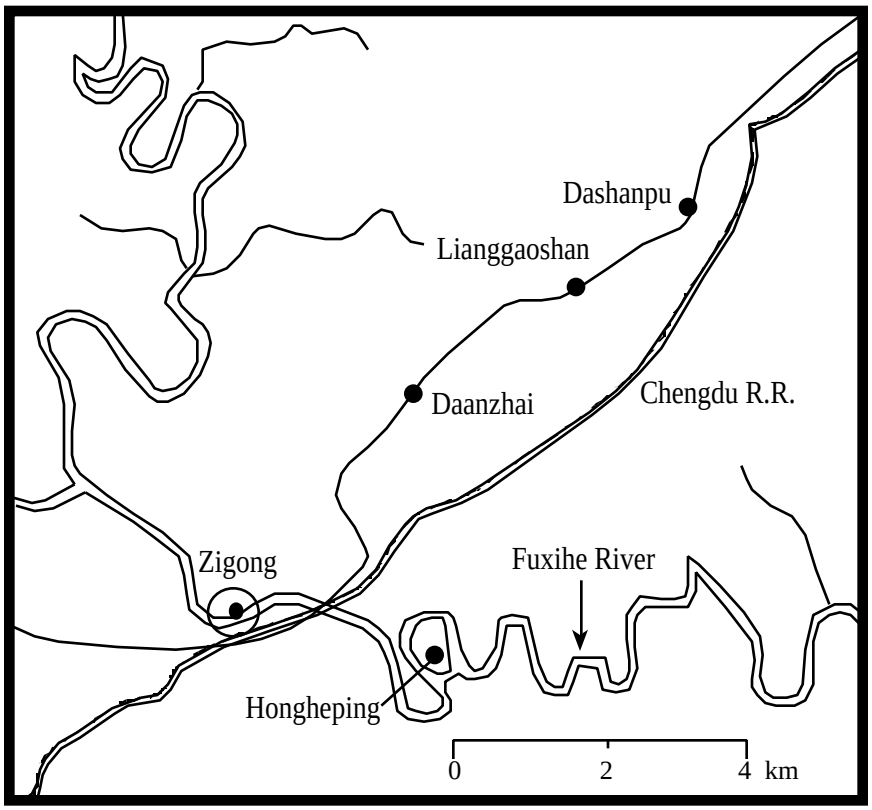

Figure 1. Locality map of the*Yandusaurus* locality near the city of Zigong.

Yandusaurus multidens and *Y. hongheensis* are recovered respectively from the upper and lower members of the Shaximiao[**] Fm. which are separated by a 3-4 m thick ostracod zone. This zone is extensively distributed throughout the Sichuan Basin, where it is recognized as a significant marker bed for distinguishing the upper and lower members of the Shaximiao Fm. The Shaximiao Fm. is the most extensive set of Jurassic redbeds in the basin and is regarded as one of the more significant units that produces dinosaurs and other fossil vertebrates. Yang et al. (1983) gave a

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[*] Translator's note: Yandu=Salt Capital, salt historically being the major economic product of the region.

[**] Translator's note: Weishampel et al., (1990) correctly transliterate but inaccurately list the upper (in Chinese = Shang) member of the Shaximiao as Shangshaximiao Fm. and lower (in Chinese = Xia) member as Xiashaximiao Fm., which are not formally recognized formational nomenclature.

preliminary report on the fauna coexisting with *Y. multidens*, but a complete taxonomic list must await further research. Associated with *Y. hongheensis* is only a single shell impression that cannot be diagnosed further than Chelonia.

Numerous fossiliferous horizons lie in the surrounding regions of Zigong where it is estimated that there are no less than five fossiliferous stratigraphic units ranging from the upper member of the Ziliujing Fm. to the upper member of the Shaximiao Fm. The most significant of these, however, are the dinosaur beds of the Lower Shaximiao around Dashanpu, and the Upper Shaximiao beds in close proximity to the ostracod zone that produce "*Zigongosaurus fuxienensis*" and *Tuojiangosaurus multispinus* in the vicinity of Shaheba Dam.

According to data from the Second Geologic Division of the Office of Geology and Mineralogy, the *Y. multidens* locality lies within the lower member of the Shaximiao Fm., 47.5 m above the Daanzhai (limestone) Member of the Ziliujing Fm. The *Y. hongheensis* locality lies over 100 m above the ostracod marker bed in the upper member of the Shaximiao Fm. Additional Ornithischia have been recovered from the Lower Shaximiao Fm. outside of the Zigong region by the Chengdu Academy of Geology at Jigong Commune in Jiangxian Co. Both size and morphology suggest this material is assignable to the genus *Yandusaurus*, but its incomplete nature prohibits a further diagnosis, and consequently it is provisionally assigned to species indeterminate.

It is not entirely clear how many *Y. multidens* individuals are represented from the Dashanpu locality, as a number of different organizations have conducted excavations there since 1973. Since 1981 excavation has been undertaken by the Dashanpu Dinosaur Division of Zigong, Sichuan. Preliminary arrangement of the fossil data indicates that over ten individuals are represented, with more expected to be unearthed in the future.

Despite the relative abundance of material, systematic description is hereby given only for two individual specimens: catalog nos. T6001 and T6001, as other individuals are represented by fragmentary limb bones or vertebrae. Although only a single individual was studied in 1979 from Jinzidang, Honghe, supplementary material has been collected by individuals from the Zigong Museum of Salt Industry in the vicinity of the type locality.

Geographic distribution of *Yandusaurus* now unexpectedly extends in a straight line northeast of Zigong for 300-400 kilometers to enter Jiangxian Co. Ranging from Middle to Late Jurassic, *Yandusaurus* is now recognized as one of the most widely distributed and abundant dinosaur taxa in the Sichuan Basin. Together with various species of stegosaurs, they comprise the most extensively distributed ornithischians in the basin.

Deep appreciation is hereby expressed to the enthusiastic support from numerous colleagues. Text figures were drafted by Deyao Huang and Weiwei Zheng; photography was provided by Shaohua Huang, Chenghe Wang, and Siping Liu. Additional assistance with manuscript transcription was provided by Shuxiang Yang, with technical editing of text and illustrations provided by Yan She and Kui Li.

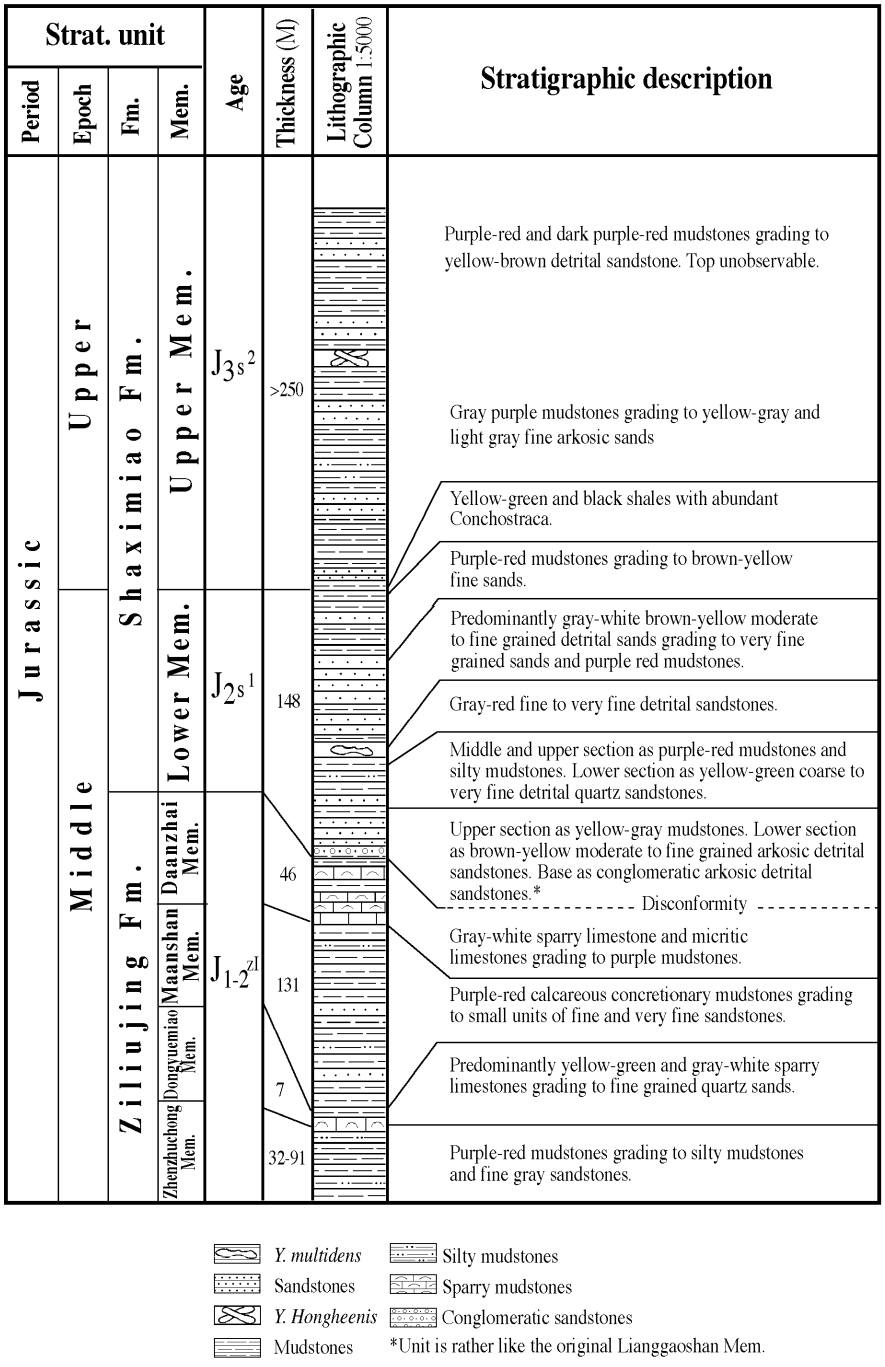

Figure 2. Stratigraphic positions of *Yandusaurus* in the Zigong region.

Section 1. *Yandusaurus multidens*

I Taxonomy

Ornithischia Seely, 1988

Ornithopoda Marsh, 1871

Hypsilophodontidae Dollo, 1882

Family diagnosis: Small cursorial ornithopods with small skull, short muzzle, orbits large and circular, premaxillary dentition typically present, and maxilla and dentary with 10-20 teeth on each side. Teeth are laterally compressed with complete enamel and well-developed marginal denticles. Canines are absent. Presacral vertebrae number 24-25, normally with 9 cervical vertebrae, and 4-6 sacral vertebrae. Cervical morphology is amphiplatyan to gently opisthocoelous. Scapula is short and dorsally broadened. Ilium is low with a long and accurate anterior lobe and a short and broadened posterior lobe. The posterior process of the pubis is long and gracile. The ischium is long and linear. The femur is shorter than the tibia with a pendent fourth trochanter situated dorsal to the midpoint of the shaft. Three metatarsals are present that exceed one-half of femur length. Distal digits are clawed.

Age and geographic distribution: Middle Jurassic to terminal Cretaceous of Europe, Africa, North America and East Asia.

Yandusaurus He, 1979

Yandusaurus hongheensis He, 1979

In 1979, at the time of nomenclature establishment, only the single species *Yandusaurus hongheensis* was known based on one specimen. Because the specimen was discovered during a phase of construction, it was subjected to enormous damage, resulting in the loss of many osteological characters. In 1981 another *Yandusaurus* species, *Y. multidens*, was discovered at Dashanpu, represented by numerous individuals, some of which are exceptionally completely preserved. Consequently, it is necessary to emend and supplement the generic diagnosis on the basis of this new material as follows:

Emended generic diagnosis: Moderately small in size with small cranium, short muzzle, and large and circular orbits. Antorbital fenestra is well developed and in outline slightly resembles an isosceles triangle. Lateral temporal fenestra is large with its ventral margin lying on the same plane as the ventral margin of the orbit. The ascending process of the maxilla is small. Premaxila is unclear, but maxillary dentition consists of 15-18 teeth. Mandibular dentition may attain 20. The anterior and posterior margins of each tooth maintain a distinct lateral keel with 3-6 denticles, but a distinct median keel is absent. 24 presacral, 9 cervical, and 5 sacral vertebrae are present. Cervical vertebrae are amphiplatyan with cervicals 4-9 posessing a well-developed ventral keel. The atlas and all posterior cervicals possess small and triangular neural arches. Dorsal vertebrae are amphiplatyan with rectangular, thin, and plate-shaped neural spines. Shoulder and pelvic girdles resemble those of *Dryosaurus* and *Dysalotosaurus.* The length of the scapula is equivalent to or shorter than the humerus. The ischial shaft is rather broadened and flattened. Anterior limbs do not attain one-half the length of the posterior limbs, and the distal portion of the posterior limbs are particularly lengthened.

Locality and age: Middle to Late Jurassic from the Jiangxian Co. region and Zigong municipality, Sichuan Province.

Yandusaurus multidens He and Cai, 1983

Type: Specimen no. T6001 (Sichuan, Zigong, Dashanpu dinosaur excavation number, as for below) is a relatively complete skeleton lacking only the anterior-most portion of the skull, majority of the mandible and posterior portion of the tail (posterior to caudal 14).

Hypodigm: T6002 is an incomplete disarticulated individual with basically complete upper and lower dentition.

Diagnosis: (slightly emended from He and Cai, 1983) A relatively small individual with a small skull that is approximately one-fifth the length of the presacral vertebrae. The muzzle is short with a small lacrimal. Orbits are large, circular, and situated slightly anteriorly with a single robust supraorbital present. Antorbital fenestra is well developed and in outline is shaped slightly like an isosceles triangle. Lateral temporal fenestra is large, slightly dumbbell shaped, nearly equivalent in height to the orbit, and with a ventral margin that lies on the same plane as the ventral margin of the orbit. The frontal is large but parietal crests are very weakly developed. The occipital crest is particularly well developed. The quadratojugal is narrow and long, the lower margin of the quadrate is flat and straight, and the ascending process of the maxilla is small. The nature of the predentary is unclear, but the lateral side of the dentary is distinctly swollen. The premaxilla is also unknown, but the maxilla contains 18 teeth, while the dentary contains 20. Enamel surrounds both the lingual and labial sides of the teeth. Anterior and posterior margins of each tooth possess distinct lateral ridges with three denticles upon each side. A medial or lateral keel is either absent or only extremely weakly developed. Vertebrae comprise 9 cervical, 15 dorsal, and 5 sacral (including no. 1 dorsosacral). Only the first 14 anterior caudals are preserved. Cervical vertebrae are amphiplatyan. Posterior from cervical 3, each neural spine is extremely small and triangular. Cervicals 4-9 maintain extremely well developed ventral keels. Dorsal centra are also amphiplatyan, are rounded and smooth ventrally, and possess thin, rectangular, and plate-shaped dorsal spines. The last two dorsals possess single capitula. Shoulder and pelvic girdles resemble *Dryosaurus* and *Dysalotosaurus*, with a short and broad scapula. Anterior lobe of ilium is gracile, long, and accurate. Posterior iliac lobe is short and broad, posterior pubic peduncle is long, obturator process is located at the proximal end of the ischium, and the shaft is relatively broadened and flat. Scapula is shorter than humeral length. Length of anterior limbs is 44-47 percent of posterior limbs, tibia is 117-118.5 percent length of femur, and metatarsus III is 57.4-62% of femur length. The lesser trochanter of the femur is lies distally and is flattened on its medial and lateral sides. From a dorsal perspective, this feature is nearly perpendicular to the proximal femur. Manus formula is 2:3:4:2?:2 with digits 4 and 5 extended in the same direction. Pes formula is 2:3:4:5:0.

Stratigraphy and geographic distribution: Lower member of the Shaximiao Fm. from Dashanpu, just northeast of the city of Zigong.

II Description

Specimens

Specimen T6001 is a nearly complete and articulated individual (Fig. 32) with no noticeable weathering. The anterior part of the muzzle is damaged, only an extremely small portion of the mandible's posterodorsal coronoid is preserved, and the middle to posterior caudals in addition to the right anterior and posterior limbs are missing.

T6002 is a slightly larger individual than T6001. The skeleton is well preserved but disarticulated and basically uncontaminated by skeletal elements from other individuals. Skull preservation includes left and right maxillae and dentaries with dentition completely preserved in the right maxilla and left dentary. Cervical vertebrae are not preserved and only a small portion of

the dorsals and caudals remain. Only a scapula represents the shoulder girdle and an ilium is all that represents the pelvic girdle. The anterior limb consists of the humerus and ulna, while a posterior limb is nearly complete.

Other individuals are represented only by isolated limb bones or vertebrae with an individual size range that falls within the range of variation for the two skeletons.

Skull and Mandible

Cranial material is only known from specimens T6001 and T6002. T6001 has a completely preserved skull articulated with its skeleton. It is unfortunate that during its collection insufficient attention resulted in damage to the right side of the skull and a portion of the muzzle. A piece of the coronoid process on the left side is all that represents the mandible. The left and right maxillae of T6002 are incompletely preserved, but both halves of the mandible are complete.

T6001 shows the cranial outline of *Y. multidens* to be extremely similar to the North American *Dryosaurus altus* (Galton, 1977), and the East African *Dysalotosaurus lettow-vorbecki* (Janensch, 1955), in that these skulls are all relatively short and high with relatively large circular orbits. Numerous cranial elements of *Y. multidens*, however, differ markedly from the latter two genera, as discussed later in the text. The most significant character of the Chinese specimens lies in their exceptionally large and rather anteriorly placed orbits and short muzzle, which consequently cause all the antorbital elements to be relatively small. Additionally, the lateral temporal fenestra is comparatively large and the quadratojugal is narrow and long, although the basic cranial-trunk ratio is relatively small with cranial length estimated to just barely exceed one-fifth the length of the presacral vertebrae. The highest point on the skull is at the posterior parietal where it is estimated to exceed one-half the total cranial length. There is a gradual inclination from the premaxilla to the posterior end of the parietal at an angle of approximately 30°. Cranial suture lines are generally distinct, except anterodorsally. Cranial elements are described as follows:

Supraoccipital: Rhomboid shaped in outline (Fig. 3-C, Pl. I-1c), this element is located posterior to the foramen magnum with its posterior margin inclined posteroventrally. At its center lies a broad and rounded glossy ridge, which gradually broadens dorsally. The element inclines laterally to both sides from the medial ridge. Its breadth is slightly larger than its height.

Exoccipital: Both left and right exoccipitals have been subjected to post-burial compressional displacement, and are consequently asymmetrically aligned. The medial side of these elements compose the lateral walls of the foramen magnum. Medioventrally these elements comprise a small portion of the occipital condyle. The ventral suture with the basioccipital is clear, as is the dorsal suture with the supraoccipital. Ventrolaterally this element becomes the paroccipital process, where no discernible suture lines are present.

Basioccipital: This element comprises a major portion of the occipital condyle; it is semicircular in outline and gently convex. Extending anteriorly, the dorsal surface contacts the exoccipital with a relatively straight suture. It projects ventrally with a very slight contraction at its center.

The occipital region of *Y. multidens* is predominantly composed of the supraoccipital, basiocciptal, and two exoccipitals. In addition, the posterior parietal and squamosal also comprise a small portion of the anterolateral side of the occiput. In outline, it is semicircular and slightly posteroventrally inclined.

Quadrate and quadratojugal: The quadrate is situated nearly vertically. Unfortunately, the articular surface has been broken. Dorsally, this element contacts the exoccipital, paroccipital process, and squamosal with a relatively thin juncture. Posteromedially it projects slightly

anteriorly to be slightly crescentic in shape. The quadratojugal is narrow and long, with an anteroposterior breadth that is one-fifth its length. It directly overlies the anterolateral side of the quadrate. This element is also crescentic in shape, projects anteriorly, and forms the posteromedial border of the temporal fenestra. There is no fenestra dorsal to the quadratojugal. The anteroventral margin of the quadratojugal contacts the jugal. The morphology, size, and relationship to the lateral temporal fenestra all differ markedly from the quadratojugals on *Hypsilophodon, Dryosaurus,* and *Dysalotosaurus,* in addition to differing from *Yandusaurus hongheensis* by being broader and shorter.

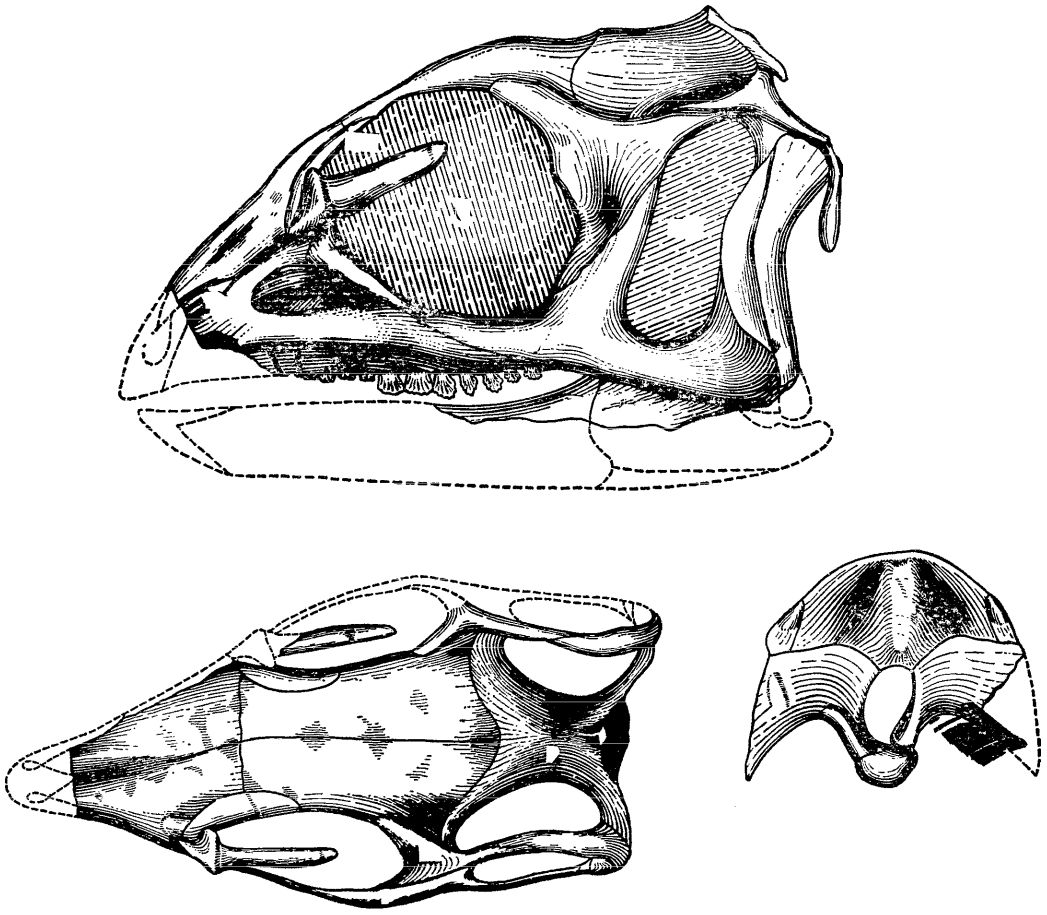

Figure 3. Skull and mandible of *Yandusaurus multidens.* Specimen T6001. A. Lateral view. B. Dorsal view. C. Posterior view (to scale). Abbreviations: Bo. Basioccipital; D. Dentary; Eo. Exoccipital; F. Frontal; J. Jugal; L. Lacrimal; Ltp. Lateral temporal fenestra; Mx. Maxilla; N. Nasal; O. Orbit; P. Parietal; Pmx. Premaxilla; Po. Postorbital; Prf. Prefrontal; Q. Quadrate; Qj. Quadratojugal; Sa. Surangular; So. Supraoccipital; Sob supraorbital; Sq. Squamosal; Stp. Supratemporal fenestra.

Squamosal: Lying posterodorsally, it projects slightly anterolaterally and is slightly concave posteriorly. The anterior process is robust and contacts the postorbital to comprise the dorsal margin of the lateral temporal fenestra and the ventral margin of the supratemporal fenestra. The two squamosal processes surrounding the dorsal portion of the quadrate are relatively small. Its outline is not entirely distinct due to conditions of preservation. The dorsal process of this element is also relatively robust and comprises a minor portion of the ventrolateral occipital crest and posterior margin of the supratemporal fenestra.

Postorbital: This element is relatively robust and triradiate anteriorly, posteriorly, and ventrally. Its proportions vary widely, with the anterior and posterior processes being relatively short, and the ventral process being relatively elongated with an acute termination. The anterior process contacts the posterolateral frontal, the posterior process contacts the anterior process of the squamosal to compose the upper temporal bar, and the posterior margin of the ventral process is in contact with the ascending process of the jugal, where at their junction, a fissure is present due to conditions of preservation. This element is surrounded by the three major fenestra of the skull: the orbit, supratemporal, and lateral temporal fenestra.

Jugal: The ventral margin is relatively flattened and straight with its anterior process extended nearly horizontally and ascending process nearly perpendicular. The posteroventral angle is in contact with the quadrate while the posteromedial portion is in contact with the quadratojugal. The general outline of this element is rather similar to *Dysalotosaurus*, but differs greatly from that on *Hypsilophodon foxii* (see Fig. 3-A).

Lacrimal and prefrontal: These two elements constitute the anterodorsal and anteroventral portions of the orbit. Both are extremely small and similar to the other cranial elements in that they are visible in lateral perspective. The suture between the lacrimal and the ascending process of the maxilla is not entirely clear; the dorsal lacrimal does not appear to curve anteriorly, and it forms the entire posterior wall of the antorbital fenestra. Prefrontal morphology resembles that on *Dysalatosaurus.* Dorsally it contacts the nasal and frontal with distinct sutures, but does not contact the premaxilla anteriorly.

Supraorbital: This is a singular, rather short and robust element. Its shaft is broad and thin, with an inflated anterior end. Between the anterior and posterior ends the shaft is distinctly constricted. The entire element extends dorsally and there is a relatively large distance between the posterior end and the posterior margin of the orbit. This element also has a distinct lateral projection, and its anterior-most surface is flat to very slightly concave. Compared to the long and gracile supraorbitals on the North American *Dryosaurus altus* and East African *Dysalotosaurus,* that of *Y. multidens* is noticeably shorter and thicker, and does not extend to the posterior margin of the orbit, which is more comparable to *Hypsilophodon foxii.* However, although both are relatively thick and short, the former differs markedly in its anterior outline.

Nasal: A depression occurs at the medial contact of the right and left nasals, with noticeable upwellings present on both sides of this depression. The anterolateral end of the nasal contacts the posterior process of the premaxilla. The medial and posterior sections individually contact the ascending process of the maxilla and prefrontal. The nasals are rather markedly expanded, but due to damage at their anterior end, their dorsal relationship to the premaxilla is not known.

Frontal: This element is relatively long and large, and constitutes approximately one-third of the total length of the skull. Medially it is slightly convex and inclines very slightly anteroposteriorly. A distinct posterior suture occurs at the contact with the parietal; an anterior suture with the nasals is indistinct, but that between the right and left frontals is clear.

Parietal: The left and right parietals are completely fused, with an extremely weak crest between them that attenuates anteriorly. This fusion is conspicuous posteriorly. Laterally the parietals are abruptly inclined to compose the entire medial walls of the supratemporal fenestrae. Their narrowest point is at the posterior quarter, while their broadest point is at the contact with the frontals. These elements are also expanded at the posterodorsal portion of the cranium, and with the projection at the posterodorsal section of the squamosal compose a particularly well-developed occipital crest.

Premaxilla: Damage to the anterior portion of the skull obscures the morphology of a large portion of the premaxilla such that only a small portion of the posterior process is present. However, it may be deduced that this element is rather small, based upon the outline of the entire skull, in addition to the abrupt inclination at the anterior nasals, which suggest that its anterior process could not have extended very far. The skull does not preserve any traces of the nares, and hence it is presumed that they are extremely small and located at the extreme anterior end of the skull.

Maxilla: The anterior maxilla has been broken, although the entire outline is basically discernible. Morphologically there is no distinct difference between this element and that of *Y. hongheensis*. The ascending process is small and inclined at approximately 45°. Dorsal to the tooth row is an anteroposteriorly extended and relatively round and smooth longitudinal projection. Foramina that generally run horizontally lie beneath this projection, but their alignment appears to be irregular. The medial morphology of the maxilla is not distinguishable, but a process on the medial side of the maxilla forms a groove with the lateral maxilla. This process should be equivalent to the medial lamina, which on *Y. hongheensis* is more well developed, to the point of completely sealing the antorbital fenestra.

T6001 cranial measurements (mm)

Preserved length of skull	82.2
Estimated complete length of skull	~90.0
Height of skull (passing through posterior margin of orbit)	44.0
Height of skull (from ventral quadrate to occipital crest)	~52.0
Length of antorbital fenestra	14.8
Height of antorbital fenestra	6.4
Length of orbit	32.3
Height of orbit	27.5
Height of lateral temporal fenestra	27.1
Greatest breadth of lateral temporal fenestra	12.0
Supratemporal fenestra anteroposterior length	20.5
Supratemporal fenestra greatest mediolateral breadth	7.0
Frontal length	40.5
Parietal length (passing through center)	16.0
Occipital height (ventral condyle to parietal crest)	33.0
Occipital breadth	~36.0

Principle fenestrae: These are consistent with a majority of dinosaurian fenestra and consist from anterior to posterior of the external nares, antorbital fenestra, orbits, supratemporal fenestrae, and lower (lateral) temporal fenestrae. The external nares have been lost although they are presumed to be rather small and located at the anterior-most portion of the skull. The antorbital fenestra is shaped nearly like an isosceles triangle but with a slightly elongated base. The posterior antorbital fenestra is formed by the lacrimal, while the anterior and ventral margin are composed of the maxillary angle. The medial side of this fenestra has been sealed by the dorsomedial lamina of the maxilla. The orbits are extremely large with their length exceeding one-third the entire skull length, and they have a nearly circular in outline, but with a length greater than height, and they are situated rather anteriorly. Consequently, the distance between the center of the orbit and the most anterior portion of the skull is less than the distance between the center of the orbit and the occiput. A sclerotic ring is not apparent. The lateral temporal fenestra is relatively high and long with its ventral end situated low. The dorsal and ventral margins approximate those of the orbit. The lower margin's anteroposterior breadth is slightly larger than the dorsal margin. In outline it is dumbbell shaped and as such the dorsal and ventral ends are broad and rounded while the center is constricted. The supratemporal fenestra is situated lateral to the parietal and is oval in shape. The medial side of the fenestra projects medially as a crescent while the lateral side is also slightly

medially concave. The initiating point at the anterior end of the fenestra and the terminal end at the posterior point of the fenestra are nearly equivalent to the initial and terminal points of the parietal angle. *Y. multidens* lacks a parietal or post-temporal fenestra.

In addition to the measurements and description provided above from type specimen T6001, data are available from specimen T6002, which consists of very incomplete maxillae from a relatively large individual. The right maxilla has suffered serious damage with nearly no aspects worthy of description except for its nearly complete dentition (Fig. 4). Observations worth noting on the left maxilla include a portion of the ascending process on its lateral side which displays the same angle of inclination as on T6001 and is as proportionally extremely small. Eight teeth are preserved on the specimen, lateral to which is a relatively broad, longitudinally directed process.

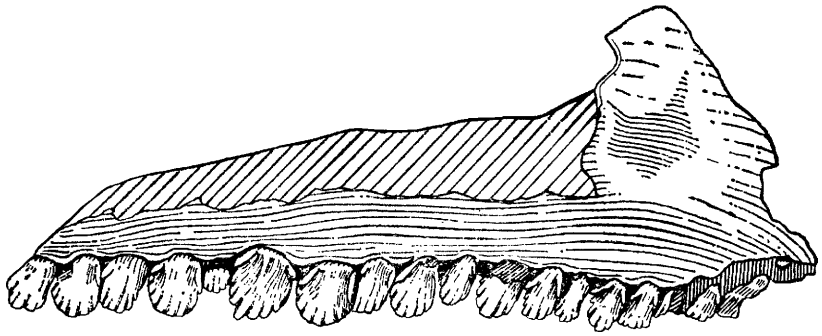

Figure 4. Lateral view of T6002 damaged right maxilla with nearly complete dentition (x2).

Dentary: Specimen T6001 preserves only a small portion of the left coronoid process, which is relatively high and broad. T6002 preserves nearly complete left and right dentaries. The left dentary is relatively robust with some slight damage anteriorly (Fig. 5-A, Pl. 1-3). The right dentary is somewhat long and gracile, with minor damage posteriorly (Fig. 5-B, C, D). During excavation it was clear that these specimens belonged to the same individual and were uncontaminated by other elements. Although the two dentaries differ morphologically, they are still regarded here as derived from a single individual. The dentary has a distinct lateral projection laterally, while lingually, at its center, it projects medially very slightly. Its ventral edge is relatively straight and flat. The coronoid process ascends directly upward. The morphology, size, and arrangement of nutrient foramen on the lateral side of the right dentary are irregular. They are distributed from the most anterior part of the mandible and extend posterior to its center. In occlusal view the dental trough is curved or slightly crescentic in shape, with its anterior portion laterally curved. The central portion is medially curved, and the posterior section is very lightly laterally curved. The length of the dental trough exceeds four-fifths the length of the entire dentary. Medially, the replacement tooth row is situated extremely high and approaches the dentition. From a medial perspective the dorsal margin of the dentary appears undulated by the alveolae with slightly sharp alveolar boundaries. The splenial has not been preserved. The Meckelian groove is located ventromedially, and begins just posterior to the symphysis. Anteriorly, this groove is relatively narrow and shallow, while posteriorly it gradually deepens, broadens, and extends to the most posterior end of the dentary. In cross-section at its center, the groove is V shaped. It is presumed that *Y. multidens* shared the character of other ornithischian dinosaurs of its time: possession of a predentary. This is supported by the morphology of the anterior end of the dentary and the relatively narrow nature of the symphysis (to date a predentary has not been found).

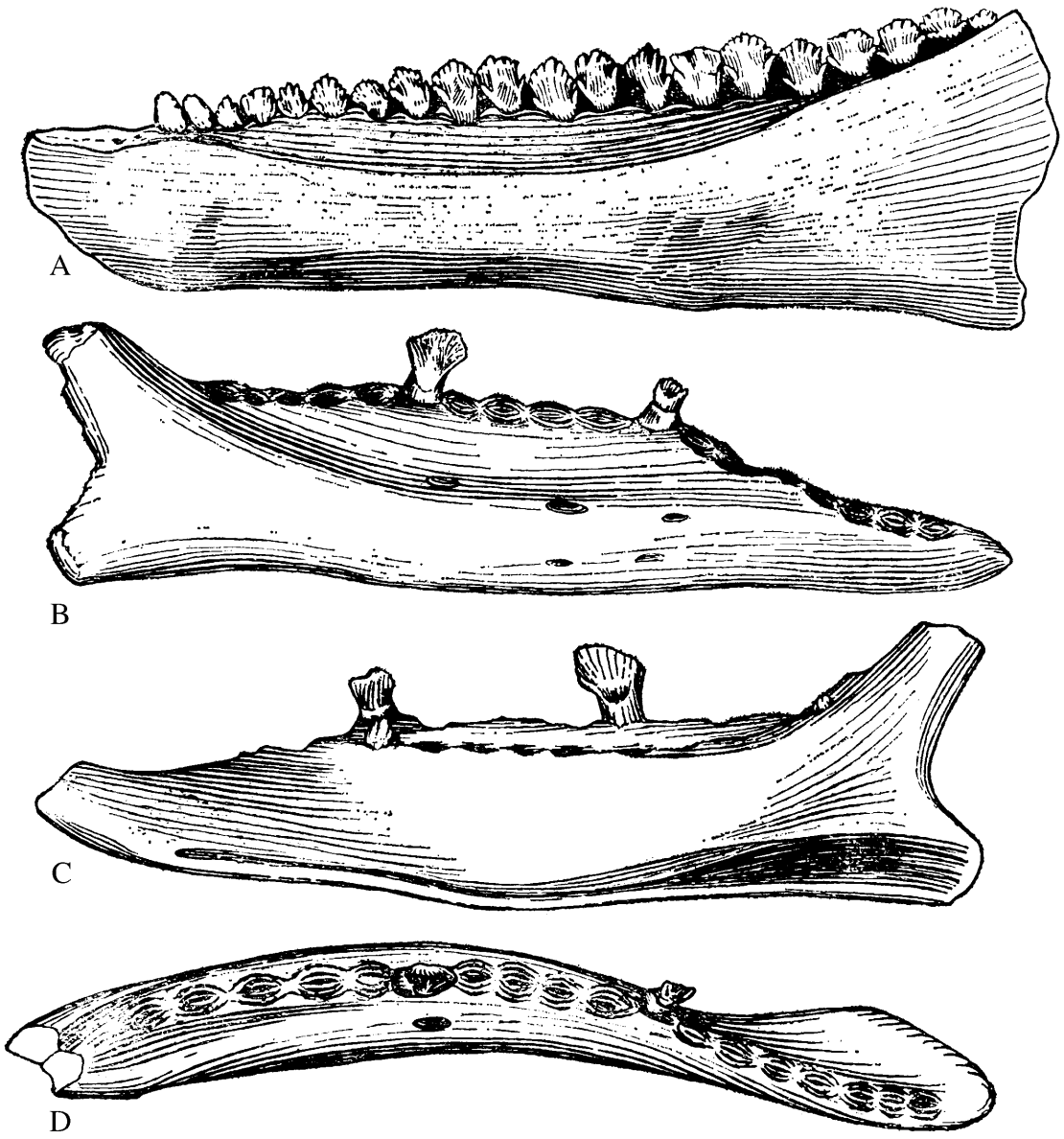

Figure 5. *Yandusaurus multidens* mandible (T6002) x2.
A. Lateral view of left mandible and dentition; B. Lateral view of right mandible; C. Medial view; D. Occlusal view.

Dentary measurements from T6002 (mm)

	Right dentary	Left dentary
Length	~70.0	~68.0
Posterior height (from most posterior alveolus)	16.0	21.2
Height at center	14.0	15.0
Length of dental trough	57.6	56.4

Dentition: The left and right dentition are preserved on T6001, although a majority of anterior teeth have been damaged. Whether premaxillary dentition was present is indeterminate. The right maxilla preserves 13 teeth, but among them only three have a complete tooth crown (P. I-2). The left maxilla preserves 11 teeth, 7 of which preserve their crowns but are still incomplete. T6002 preserves a complete dental sequence in its right maxilla, although the first two teeth are represented by roots, and the fifth tooth from the end is not fully erupted. The left maxilla preserves 11 teeth, of which 7 have visible but incomplete crowns. The left mandible of T6002 displays the most complete dentition with 20 completely erupted and nearly undamaged teeth. Only two teeth are preserved in the right mandible of T6002.

The material listed above indicates a maxillary dentition of 18 and a mandibular dentition of 20, with the condition of the anterior dentition unclear. The principle characteristic of *Y. multidens* dentition is the large dental count, with maxillary and mandibular dentition exceeding all other taxa in the Hypsilophodontidae (see Table I). However, the number of denticles is small, not exceeding seven, with three at each anterior and posterior edge and one at the top of the tooth. Each tooth also displays a very basal and very distinct lateral ridge anteriorly and posteriorly. Both maxillary and mandibular teeth either completely lack, or at most have developed only an extremely weak lingual or labial median keel. These characters are taxonomically significant for the species. Furthermore, enamel completely surrounds the teeth, morphology is not heterodont, and a caniniform tooth is absent. The crowns are higher than broad, particularly on the lateral sides which are higher than the lingual sides. Dental alignment is dense, distinct interdental vacuities are absent, and teeth are slightly imbricated. Maxillary dentition is shorter than mandibular dentition.

The best preserved maxillary dentition is on the right side of T6002 with anterior and posterior teeth being comparatively smaller. Teeth posterior to the center appear to be the largest. Each tooth is slightly inclined posteriorly and all are morphologically similar. Denticles are distinct but short; that is, they do not extend very far longitudinally before terminating. The enamel surface has nearly parallel striations. A median keel is absent, but an extremely short lateral ridge is present on both sides of the base of the crown which extends for a very short distance ventrolaterally before terminating. This dentition does not differ markedly from that of *Y. hongheensis*, although *Y. multidens* has a higher dental count (18 vs. 15) with fewer denticles.

Table 1. Dental count of some primitive ornithischian dinosaurs

	Premaxilla	Maxilla	Mandible
Heterodontosaurus tucki	3	12	?
Dianchungosaurus lufengensis	3	?	12-13
Tawasaurus minor	~5	~12	?
Tatisaurus oehleri	?	?	18
Echinodon becklessii	3	~11	10
Nanosaurus agilis	?	?	13
Lesothosaurus diagnosticus	6	~14	~14
Pisanosaurus mertii	?	11+ (17-18?)	15
Zephyrosaurus schaffi	5	14-15	?
Hypsilophodon foxii	5	10-11	13-14
Dysalotosaurus lettow-vorbecki	0?	13	11-12
Yandusaurus hongheensis	?	15	?
Y. multidens	?	18	20

The left mandible of T6002 displays the best-preserved mandibular dentition, being nearly complete and erupted, with the exception of the most posterior semi-erupted tooth. Some (nos. 9, 12, 13, 14, 17) have undergone dental wear, suggested by a central spatulate-shaped trough dorsolaterally. There is no strong distinction between the morphology of the lower dentition and that of the upper. Anterior teeth are extremely small; they enlarge posteriorly from tooth 1 to reach maximum size between teeth 13 and16. From this point posteriorly the dentition again diminishes in size. The combined length of alveolae 1-2 is equal to the length of tooth 15. The height of tooth 1 or 2 is less than one-half the height of tooth 15. The dentition is densely packed, to the point of several teeth being imbricated. Number of denticles, length, and position of lateral ridges are equivalent to the upper dentition. However, the mandibular dentition does have some characteristic features that differ from the upper dentition, the most noticeable being teeth 1 and 2, which appear bluntly conical with clearly pointed crowns, display vague denticles, and lack lateral ridges. These characters differ markedly from both those in the upper dentition and the rest of the mandibular dentition. Teeth 3-7 resemble those posteriorly; however, the lateral crown is slightly lower and they lack distinct lateral ridges and medial keels. Mandibular denticles are deeper than those on the maxilla and the parallel striations are more vague. Laterally and basally the teeth are conspicuously swollen.

Dentition measurements (mm)

Dentition length of T6002 right maxilla	~51.0
Dentition length of T6002 left mandible	58.4
Dentition length of teeth 1-7 on left mandible T6002	16.3
Dentition length of teeth 11-17 on left mandible T6002	24.5
Lateral height/width ratio of tooth 13 on T6002 left mandible	70%
Lateral height/width ratio of tooth 7 on T6002 right maxilla	56%

Vertebrae

Specimen T6001 displays 43 well-preserved articulated vertebrae consisting of 9 cervicals, 15 dorsals, 5 sacrals, and 14 caudals.

Cervical vertebrae: The complete articulated series from the proatlas to cervical vertebra 9 on specimen T6001 may be observed (Fig. 6, Pl. I-7), with various degrees of damage on only a small portion of centra, neural spines and cervical ribs.

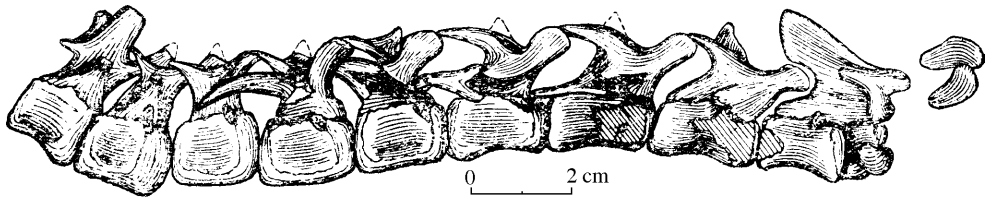

Figure 6. Right lateral view of cervical to dorsal vertebra 1, and dorsal (right) view of proatlas on T6001 *Yandusaurus multidens* (x 2/3)
Abbreviations: P. proatlas; C. cervical; D. dorsal.

Atlas-axis complex: Left and right proatlas, atlas intercentrum, odontoid process, and neural arch are present in addition to axis intercentrum, centrum, neural arch and spine. Although the proatlas lies anterodorsal to the neural arch, the elements have been slightly shifted and are not in direct articulation. The right proatlas is slightly shifted to the left. Its morphology (Fig. 7, Pl. I-4) generally resembles that on *Hypsilophodon foxi*, being slightly triangular in outline, laterally compressed, appropriately anteroposteriorly extended, rather flat and straight medially (length 11.5 mm), with the posterolateral side (length 8 mm) slightly longer than anterolateral side (length 6.5

mm). The anterior angle is 41°, posterior angle is 24°, and lateral angle is 115°. The three angles are all well rounded. The dorsal surface is rather flattened, although the posteriorly extended section is slightly inclined laterally and turned upward. The ventral surface is not flat and in the middle of the posterolateral side there is a tuberosity parallel to the posterior side that gradually attenuates toward the posterior and lateral angles. The lateral side is precipitous but the medial side is gently curved. A low sulcus lies between the anterolateral side and medial margin. The general condition of the proatlas resembles a triangle that is thickest at the center of the posterolateral side, relatively thick anteriorly, and relatively thin at the center of the posteromedial side.

Figure 7. Dorsal view of the proatlas of *Yandusaurus multidens* (T6001) (x 1.4).

The atlas is composed of an intercentrum, odontoid process, and neural arch. The intercentrum is completely preserved (see Fig. 8A-E, Pl. I-6), and measures 14.5 mm laterally, 7.5 mm anteroposteriorly, and 8 mm high. In anterior perspective it is slightly crescentic in shape. The dorsal articular surface for the odontoid process is a crescentic depression with nearly perfectly rounded sides and a low and flat longitudinal ridge at its center. On both sides of this ridge a shallow elliptically shaped depression extends laterally with even smaller indentations lying near the longitudinal ridge. Laterally these depressions are relatively smooth. The anterior end of the intercentrum articulates with the occipital condyle with a crescentic articular surface that is transverse and anteroventrally inclined. The ventral side of this element is slightly rectangular and perfectly rounded laterally. A low and relatively spacious platform lies at its center, which becomes slightly narrowed posteriorly. A shallow transverse elliptical depression containing several small rounded indentations lies at the posterior end of this platform. Both posteroventral sides of the intercentrum articulate with the posteroventral margin of the centrum to compose two processes that facilitate articulation of the first cervical rib. A shallow anteriorly inclined trough separates the processes from the ventral platform. The posterior end is slightly convex, crescentic in shape, and at the center of its ventral region articulates with the axis intercentrum, while dorsally it articulates with the centrum. The odontoid process is rather robust and situated dorsal to the atlas intercentrum and anterodorsal to the axis intercentrum with a length of 8 mm and width of 9 mm. The anterior end is strongly projected while posteriorly it fuses to the axis centrum with a flat surface. Ventrally it is rounded and smooth with a very slight constriction at its center. The posterior surface of this constriction articulates with the dorsal surface of the atlas. The dorsal surface of the odontoid process is relatively flat and slightly spatulate in shape. Medial depressions lie laterally. The morphology of the atlas neural arch (Fig. 8-F, Pl. I-5) resembles a broadened “T” that is laterally convex and medially concave with a relatively flat and straight dorsal end that is extended anteroposteriorly, and anteroventrally. It is most robust ventrally, highest posteriorly, and anteriorly, where it is slightly convex laterally and slightly concave medially, it is composed of thin laminae. The neural arch is situated dorsolateral to the odontoid process, because the right neural arch is slightly dislocated from the atlas intercentrum. However, the left arch articulates directly with the dorsal atlas intercentrum.

The axis intercentrum is an exceptionally small wedge-shaped piece located anterolateral to the axis and posteroventral to the atlas intercentrum. It narrows anteriorly, it is 6.4 mm in breadth, and 4 mm in both length and height. An anteriorly inclined lenticular articular surface facilitates the anterior articulation with the flat surface of the atlas intercentrum, and here, at its anteroventral margin, it comprises a laminar ridge. The posterior end and ventral surface are slightly inclined lenticular bodies. The anteroventral and posteroventral margins display very weak medial depressions. Posteriorly, the articular surface for the axis is slightly convex.

The anterior and posterior ends of the axis centrum are flat but the surface for articulation with the atlas intercentrum is slightly concave posteriorly, resulting in a slight posterior inclination of the anteroventral region. The ventral surface is rounded, smooth, and lacks a keel. Neural arch

and spine do not differ noticeably from *Hypsilophodon*. The neural spine is well developed, ascends posterodorsally, and is slightly concave dorsomedially. Diapophyses are weakly developed and situated at the center of the neural arch and centrum fusion point.

Figure 8. Atlas of T6001 *Yandusaurus multidens* (x 1.5).
A-E atlas intercentrum; A. anterior; B. posterior; C. dorsal; D. ventral; E. right lateral; F. right lateral neural arch.

Cervicals 3-9: These seven vertebrae are well preserved, with the exception of some damage sustained to the anterior right side of centrum 3, and the anterior portions of centra 4 and 5. Posterior to Cv4 there is no large discrepancy in cervical morphology or size. Centra are all amphiplatyan, and parapophyses are located anterodorsally on the centrum, or at the anterior end of the conspicuous neural arch and centrum suture line. The dorsal spine is small and triangular. Postzygopophyses are slightly higher than prezygopophyses. A well-developed ventral keel is present on cervical centra 4-9.

Cv3 is amphiplatyan and has the longest, smallest diameter centrum among the cervical series (see Table 2). The centrum is distinctly laterally constricted at its center, causing it to be angular in ventral perspective. This angle extends from the anterior to posterior end with its sharpest point at its center and then gradually broadening anteroposteriorly. It is noticeably broader posteriorly than anteriorly. Parapophyses lie anterodorsally on the centrum. Diapophyses are short and small, located ventral to the neural arch, and extend slightly posteroventrally. Prezygopophyses are distinctly anteriorly projected with a slight angle of dorsomedial inclination, are situated slightly lower than the postzygopophyses, and possess larger articular surfaces than the postzygopophyses. The neural spine is triangular and dorsally rounded with an anterior margin that is inclined anteriorly at a rather precipitous angle.

Cv4-5 display centra that distinctly differ from Cv3 by their conspicuous ventral keel and larger and longer posteroventrally directed diapophyses positioned slightly lower on the neural arch. Diapophyses on Cv5 have migrated to the center of the neural arch. Prezygopophyses are shortened and inclined anterodorsally while postzygopophyses are lengthened. Cv4 maintains pre and postzygopophyses of equivalent height, but Cv5 has prezygopophyses slightly higher than the postzygopophyses, which are the longest in the series. The centra of both are shorter than on Cv3.

Cv6 displays an irregularly hexagonal anterior end and nearly circular posterior end. The mediolateral constriction of the centrum resembles a broadened concave band. A conspicuous keel, which lies ventrally, is narrow in its center and broadened anteroposteriorly. The neural canal is large and elliptical due to compressional deformation, which has also affected the relatively robust diapophyses, causing them to be asymmetrical with the right posterodorsally extended, and the left posteroventrally extended. In reconstruction, they may both be posteriorly extended on a single plane. Prezygopophyses are further shortened and inclined slightly anterodorsally with large and flat nearly elliptical articular surfaces. The length of the postzygopophyses is slightly less than that of Cv5. The breadth between pre- and postzygopophyses articular surfaces is equivalent. The neural spine is small, triangular, and sharply pointed, and displays a nearly vertical anterior margin.

Cv7-8 resemble Cv6 and differ only in the ascension of their parapophyses; the position of the diapophyses has moved higher up the neural arch, postzygopophyses have become shortened, and the ventral keel has become broadened.

Cv9 has the shortest centrum in the series with a nearly circular anterior end, weaker lateral depressions, and a slightly narrower ventral keel than Cv8. Parapophyses lie anterolateral to the neural arch and anterodorsal to the centrum, with a large portion lying on the neural arch. Diapophyses are relatively long and from a dorsal perspective are nearly rectangular. Due to distortion, the right diapophysis extends dorsolaterally and the left extends ventrally. In reconstruction they would lie on the same plane or extend slightly dorsally. Postzygopophyses are shorter than Cv8 with articular surfaces narrower than those anterior to them. The top of the neural spine is broken but the entire element may be recognized as triangular.

Morphologic variation in cervicals 3-9 occurs by a gradual shortening of the centrum, and a gradual broadening of the ventral keel, with the broadest occurring on Cv8; diapophyses gradually ascend the neural arch, increase in length, and change direction of extension from posterior and slightly ventral to slightly posterolateral and parallel, or with a very slight posterodorsal inclination. Prezygopophyses gradually shorten; postzygopophyses gradually lengthen and become longest at C5, whereas posterior to this point they once again gradually shorten (see Table 2).

Cervical ribs: These are partially preserved and all sustained some damage. Rib 1 is holocephalous with a thin and flat shaft that is robust at its center and gracile at both ends. Posteriorly it may have extended to the anterior portion of the Cv3 centrum. Preserved length is 25 mm. Rib 4 is short with a thin and flat capitulum and tuberculum. It is straight with a slightly club-shaped shaft that attenuates posteriorly. The right rib's preserved length is 17 mm and it extends nearly horizontally posteriorly, while the left rib is extended posteroventrally. Right rib 5 also extends nearly horizontally to the posterior, but right rib 6 is extended posteroventrally and displays an expanded and flattened shaft. Ribs 7-9 are posteroventrally extended and ribs 8-9 are the largest and longest in the series with distinctly broadened, thin, and flat capitula and tubercula, and shafts that are slightly convex laterally and slightly concave medially. Cross-sections at midshaft are kidney shaped. Breadth and thickness of the shafts gradually diminish dorsoventrally.

Each of the ribs gradually increase in size and length posteriorly as does the distance between the capitulum and tuberculum. Their posterior projection gradually transforms from being horizontal to semi-ventral.

Dorsal vertebrae: All 15 articulated dorsal vertebrae are preserved on T6001 (see Pl. II-2), and the right side preserves all the ribs, although a portion of them are damaged distally. On the left side only a portion of proximal ribs are preserved. T6002 preserves five dorsal vertebrae (representing one anterior, two medial or posterior, and two posterior), all of which have lost their centra.

All 15 dorsal vertebrae of T6001 have been subjected to compressional distortion with centra that have shifted slightly dorsally and to the left. On the right side diapophyses are inclined dorsally while on the left side they are inclined ventrally. Neural spines also incline slightly to the left. Because distortion has occurred uniformly, the morphology and series recognition are unaffected.

The dorsal-cervical boundary is recognized between the ninth and tenth presacral vertebrae on specimen T6001, based upon notable distinctions. The ninth presacral maintains typical cervical characteristics as opposed to the tenth presacral which is distinctly dorsal in nature. Both lack transition phase characters as exemplified by the ninth presacral possessing a typically cervical conspicuous ventral keel, which has become lost on the tenth presacral. Moreover, the former

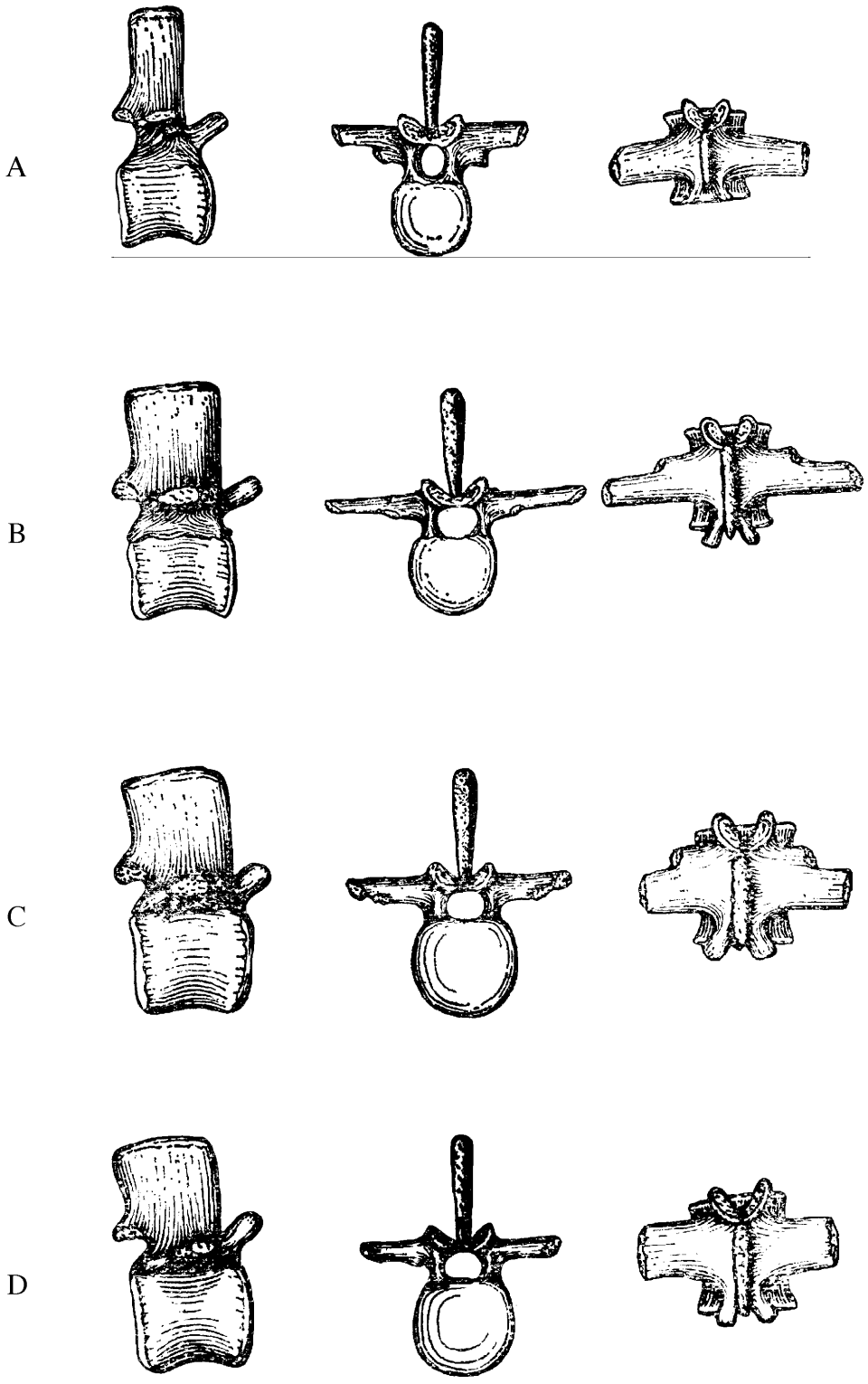

Figure 9. Dorsal vertebrae of T6001 *Yandusaurus multidens* (to scale). A. D2; B. D8; C. D12; D. D13. Left. Right view; Center. Anterior view; Right. Dorsal view.

displays a small triangular neural spine, which on the latter has become noticeably enlarged into a narrow rectangle. Parapophyses lie anterodorsally on the former while on the latter they have migrated anteroventrally to the base of the diapophyses. Diapophyses are also noticeably lengthened and broadened, and particularly noticeable are the ribs, with capitula which have transformed from the posterior cervical style to the typical dorsal mode.Dorsal vertebrae of *Yandusaurus multidens* and *Y. hongheensis* are similar in morphology, being amphiplatyan, round and smooth ventrally, centrum nearly circular anteriorly and posteriorly, anterior and posterolateral ends of centrum display short and weak longitudinal striations, a distinct suture line delineates the neural arch from the centrum, diapophyses are horizontal or slightly inclined dorsally, and neural spines are a thin rectangular plate.

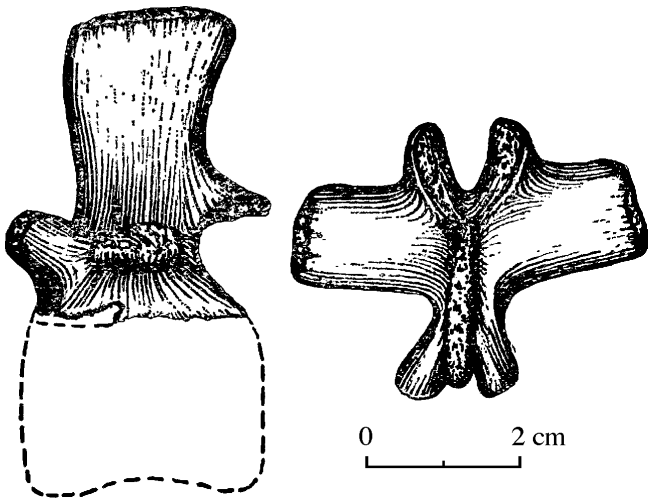

Figure 10. Dorsal vertebra 13 of T6002 *Yandusaurus multidens* (to scale). Left. Left lateral view; Right. Dorsal view.

Dorsal vertebrae 1 of T6001 has a centrum with nearly circular anterior and posterior ends, a clearly constricted medial section, a slightly laminar ventral surface that lacks a keel and a high neural arch. Parapophyses are situated anteroventral to the base of diapophyses and in dorsal outline resemble *Hypsilophodon*, but are not as robust. Prezygopophyses are short with anterodorsally directed articular surfaces. The neural spine is a narrow rectangle.

D2 (see Fig. 9-A) maintains a round and smooth medial centrum with short and weak longitudinal striations at its anterior and posterior ends. The neural canal is relatively small and slightly longitudinally elliptical. Parapophyses are situated anteroventral to the diapophyses, which are nearly rectangular, and compared to D1 are more broad and robust with the right side distorted dorsally and the left side distorted also slightly dorsally. The neural spine is a narrow rectangle but is slightly broader than on D1.

D3-7 display centra that are all slightly shorter and smaller than their anterior and posterior counterparts. Neural arches gradually diminish in height anteroposteriorly, diapophyses consecutively enlarge and lengthen, parapophyses gradually migrate from anteroventral to anterior on the diapophyses, and neural spines increase in height and breadth posteriorly.

D8 (see Fig. 9-B) is enlarged and lengthened compared to its anterior counterparts. The neural arch is slightly low with a transversely elliptical neural canal. Parapophyses lie anteroventral to the center of the diapophyses, which in dorsal view approximate a long triangle, and constitute the longest in the series. The right diapophysis is dorsally inclined but on the left side it is ventrally inclined. The neural spine is rather broad.

The centra of D9-11 are all more robust and longer than D8, but the lengths of the diapophyses gradually diminish, although their breadth constitutes the largest in the series. The parapophyses have been shifted somewhat laterally, and the neural spines have been broadened very slightly compared to D8.

The centrum of D12 is more robust than the several anterior to it. The diapophyses are short and relatively broad, and parapophyses are located anteromediolaterally (see Fig. 9-C).

The centrum of D13 is even more robust than on the vertebrae anterior to it, and the diapophyses are further shortened with noticeably broadened terminations. Remnant parapophyses lie only anteriorly near the end of the diapophyses with small articulation surfaces.

D14-15 (see Fig. 9-D) are the most robust in the dorsal series with short, thick, and strong slightly rectangular diapophyses that have only a single elliptically shaped concave surface for articulation with the capitulum. Clearly the parapophyses have become lost on D14-15.

Posterior morphologic variation of the dorsal vertebrae of T6001is shown by their sequentially becoming larger and longer with a gradual height reduction of the neural arch. The neural canal transforms from longitudinally elliptical to transversely elliptical; diapophyses gradually increase in length and breadth, attaining maximum length on D8, and they become shorter and thinner again posteriorly. The parapophyses migrate anteriorly and laterally from the anteroventral side of the diapophyses, with D13 maintaining only remnant parapophyses at the terminal end of the diapophyses. The parapophyses have become lost on D14-15. Prezygopophysis articular surfaces alter from dorsal to dorsomedial inclination. Neural spines are all rectangular, with the anterior three being narrow and gradually increasing posteriorly in breadth (Table 3).

Although the dorsal vertebrae of T6002 lack centra, the dorsal portion of the vertebrae are either undistorted or distorted very slightly such that they may serve as supplemental descriptions. The diapophyses of D1 (or D2) are slightly rectangular in shape with a length of 21 mm, breadth at base of 17 mm, and breadth at terminal end of 8 mm. The dorsal surface is slightly dorsally bowed with a very shallow groove lying at the anterior and posterior margins. An inflated ridge lies on the ventral surface. Parapophyses are situated anteroventral to the proximal end with a relatively flat and laterally inclined articular surface. The dorsal inclination of the right diapophysis may be the result of compressional distortion. The neural arch is narrow and 12 mm broad at its base.

Two posteromedial dorsal neural spines are relatively well preserved, and characteristically similar. The neural canal is transversely elliptical, and diapophyses are broad, slightly triangular, and slightly dorsally extended. Parapophyses and diapophyses articular surfaces are equivalent in size. The neural spine is low and rectangular, slightly higher than broad, and has a slightly crescentic dorsal end with a relatively straight anterior margin and slightly anteriorly projected posterior margin. The breadth between prezygopophyses is slightly larger than between postzygopophyses.

D13 has robust horizontally extended diapophyses (see Fig. 10) with nearly elliptical, and medially saddle-shaped, articular surfaces at their terminal ends. Parapophyses are placed anteroventrally very near to the terminal ends of the diapophyses.

D15 has particularly robust diapophyses with slightly concave elliptical surfaces at the terminal ends. Length is 12.5 mm and height is 9.5 mm. The parapophyses are completely lost. The neural spine is a broad and low rectangle.

Dorsal ribs: T6001 preserves relatively good material with all of the ribs preserved on the right side, and numbers 1-3 in relatively good condition. Varying degrees of breakage have occurred on the distal ends of the remaining ribs. The left side only preserves a small portion of proximal ribs. T6002 preserves only one complete left dorsal rib.

On T6001 the three anterior ribs are longest (see Table 3). Dorsal ribs 2-3 are robust but posteriorly ribs gradually become more gracile and reduce in length. Degree of curvature among the dorsal rib series is unclear, as the more linear nature of the medial and posterior ribs may be due to taphonomic conditions. Dorsal rib 1 is long. At the proximal end of the shaft there is a longitudinal anteriorly convex lamina such that in cross-section the element is triangular. Distally the element gradually becomes thin and flat, and terminates with a very slight broadening. Shafts of dorsal ribs 2-3 are more broad with a more robust laminar ridge. Ribs 9-11 have short and gracile shafts. Ribs 14-15 are short with robust holocephalous and elliptical capitula and a shaft that rapidly becomes gracile.

T6002 has only a single left dorsal rib 3 or 4 (see Fig. 11) which is relatively long and robust with a broad, thin, and flat shaft at the articular region. Medially there is a broad and shallow groove, proximolaterally there is a conspicuous laminar ridge, and distally the shaft is thin and flat. Articular surfaces of the capitulum and tuberculum are nearly circular, with the latter larger than the former.

Figure 11. Anterior view of T6002 *Yandusaurus multidens* left dorsal rib (to scale).

Sacrum: T6001 preserves five fused sacral vertebrae (see Fig. 12, Pl. I-8, II-2). T6002 does not preserve this element.

Utilizing the entire vertebral sequence of specimen T6001, the sacral-dorsal boundary is recognized between vertebrae 24-25, with no. 24 representing dorsal 15 and no. 25 representing sacral 1, and the two are distinctly characteristic. Sacral 1, with the exception of its relatively gracile ribs that do not fuse with the sacracostal nodes, clearly lies within the sacral vertebrae morphotype.

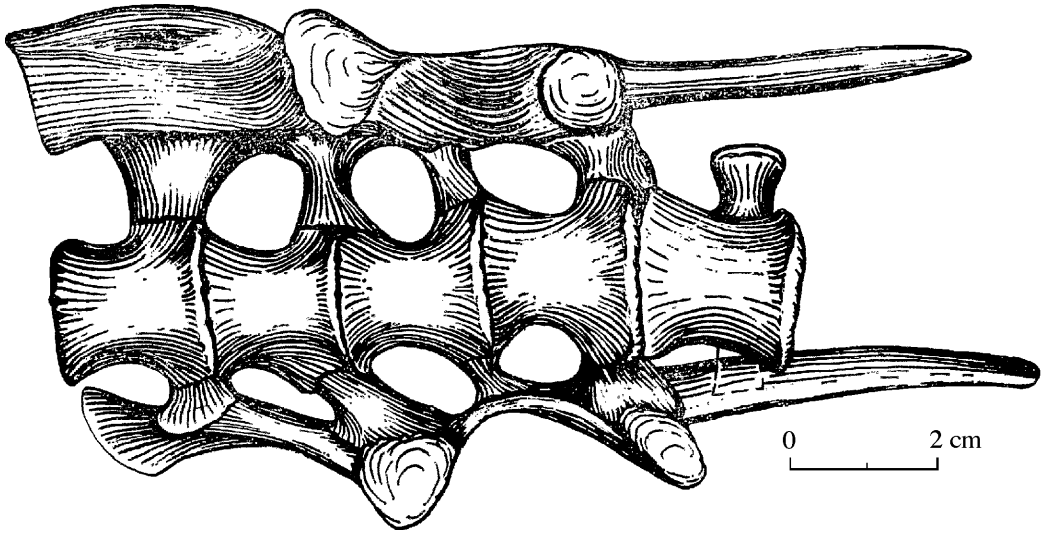

Figure 12. Ventral view of T6001 *Yandusaurus multidens* ilia and sacral vertebra (to scale).

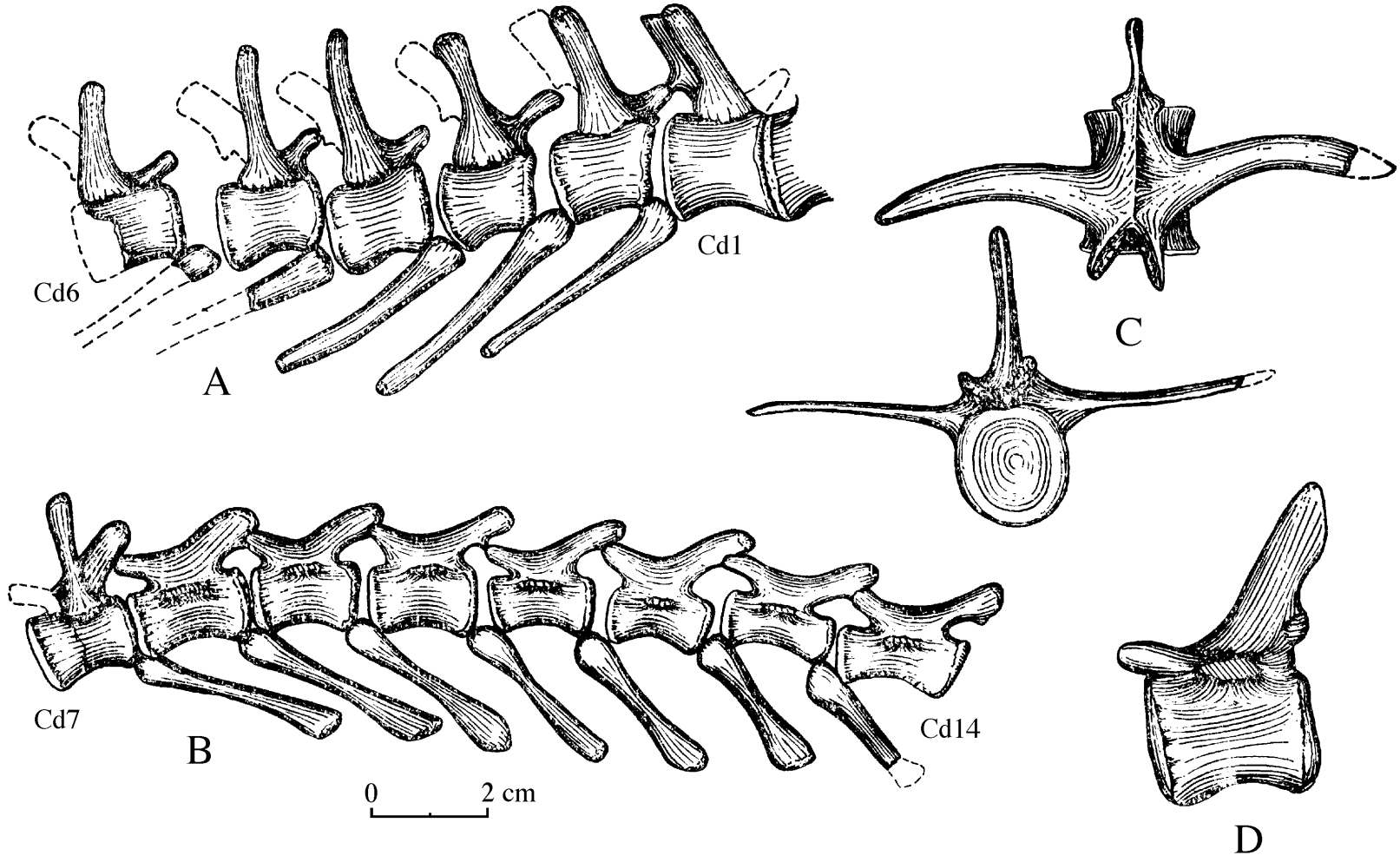

Figure 13. Caudal vertebrae and cheverons of *Yandusaurus multidens* (x 9/10)
A. Lateral view of caudals 1-6 with chevrons (T6001). B. Lateral view of caudals 7-14 with cheverons (T6001). C. Anterior and dorsal views of caudal 2 or 3 (T6002). D. Lateral view of caudal 5 or 6 (T6002).

Within the sacral column, all centra are fused but their intercentra boundaries are still conspicuous, with anterior and posterior ends both enlarged and heightened in a transversely elliptical shape. Sacral ribs are massive, and with the exception of S1, the remaining ribs all connect with the ilia. Neural spines are high, broad rectangles. S5 has the largest centrum.

The S1 centrum is robust with its anterior end nearly elliptical transversely and posterior end kidney shaped with a rough uneven articulating surface that is closely associated with the anterior end of S2, or fused. This centrum possesses two elliptically shaped articular surfaces posterodorsolaterally which contact counterparts at the anterior end of S2. The medial section of the centrum is slightly constricted; ventrally it is rounded and smooth, with the anteroventral margin displaying short and weak longitudinal striations. Sacral ribs (diapophyses) are gracile and unconnected to the ilia. A distinct suture lies between the neural arch and centrum. The neural canal is large and transversely elliptical posteriorly. The neural spine is nearly rectangular and slightly broader than high. One could consider S1 as a dorsal and not sacral vertebra based upon the character of its relatively gracile ribs that are unconnected to the ilia. Hence, S1 may be regarded as a transitional dorsosacral vertebra.

The centrum of S2 is larger than S3, transversely expandedanteriorly, constricted at its center, and less expanded posteriorly. The anteroventral surface is broad and slightly convex medially. At each side is a laminar ridge that extends anterolaterally but attenuates posteriorly at the middle of the centrum. The posteroventral surface is narrow with a short, broad, and shallow longitudinal trough at its center. The sacral ribs are short and thick with a large portion of them in contact with the anterolateral sides of the centrum and a small portion of them also in contact with the posterolateral ends of S1. Distally, they contact the medial side of the iliac pubic peduncle. The neural canal is large and lenticular. The neural spine is rectangular, broader than high, and is the broadest in the vertebral series (see Table 4).

Ventrally S3 has a medial trough that is more conspicuous than the medial trough on the centrum anterior to it. Sacral ribs are small and located anterolaterally; distally they contact the medial side of the acetabular margin.

The S4 centrum is larger than S3 with an indistinct longitudinal trough ventrally. The sacral ribs are relatively robust and distally they contact the medial side of the ischiac peduncle. The neural spine is fused to those anterior and posterior to it.

The S5 centrum is constricted posteriorly with a nearly circular distal end. Ventrally there is a shallow and narrow longitudinal trough. Sacral ribs are large and thick; distally they incline dorsally and fan out to contact the anteromedial side of the posterior iliac lobe. The neural canal is relatively small, appearing semi-elliptical in posterior perspective. The neural spine is almost square in shape.

Caudal vertebrae: T6001 preserves 14 articulated anterior caudals (see Fig. 13-A, B, Pl. II-3, III-1). All centra are in tight original articulation with the exception of caudals 4-6 which have shifted slightly in position. The Cd6 centrum has suffered some damage. Haemal arches have been preserved in position except for arch 6, which has been lost, and there is some slight damage to arches 4, 5, and 7. Specimen T6002 preserves four anterior caudals and their haemal arches, and one medial caudal with two haemal arches.

The first caudal and last sacral differ distinctly . The sacral centrum is more robust than the caudal, the sacral ribs are broad and massive and fused to the ilia, and the caudal ribs (or diapophyses) are gracile, long, and not in contact with the ilia. The sacral neural spine is broadly expanded, square, and nearly upright, while the caudal is narrow, long, and posteriorly inclined.

Particularly worth noting is the presence of the first haemal arch on the posteroventral centrum of the first caudal.

Compressional distortion has occurred on the diapophyses of T6001's 14 caudals causing the right side to be dorsally extended and the left side to be ventrally extended. Centra are amphiplatyan with very slightly concave posterior ends; they display slight medial constrictions, have a very weak longitudinal keel ventromedially, and a smooth and unornamented lateral and ventral surfaces. The neural spines incline posteriorly. The articular surfaces on posterior haemal arches are larger than the anterior surfaces.

Cd1 has a large and thick centrum with short and faint longitudinal striations anteroventrally. At the posteromedial section there is a faint longitudinal keel. Anteriorly the centrum is nearly circular. The diapophyses are narrow, long, and shaped like a thin plate. In reconstruction they should be horizontally extended. The neural canal is elliptically skewed due to compressional distortion. The neural spine is narrow, long, and posteriorly inclined at a 70° angle.

Cd2-5 have relatively well-preserved centra and diapophyses, but Cd6 has a broken posterior centrum. Cd2-6 are similar in character with amphiplatyan centrum, a slightly posteriorly inclined ventral surface, a distinct longitudinal median keel, and nearly circular anterior and posterior ends. Centra are laterally smooth and lack ornamentation, with well-developed anterior and posteroventral surfaces for haemal arches. The posterior haemal arch surface articular surface is larger than the anterior surface and the suture between the haemal arch and centrum is still recognizable. The diapophyses are long and thin and positioned dorsally to the basal neural arch suture, with proximal ends slightly broadened and gradually narrowing distally. Pre- and postzygopophyses are relatively small with prezygopophyses in the anterior series anterodorsally projected and larger than the postzygopophyses. Postzygopophyses on Cd2-6 gradually migrate dorsally toward the neural spine.

Cd7-14 centra become sequentially thinner and slightly longer posteriorly. The anterior and posterior ends of centra are nearly circular. The ventral longitudinal keel is narrower but still clear. The neural arch-centrum suture has become lost. Diapophyses are gracile, thin and flat. On Cd7 the diapophyses are longer than the neural spine, but from Cd8-14 the diapophyses gradually shorten and narrow. On the left side they are horizontal and slightly extended posteriorly. On Cd14 the diapophyses length is 6.5 mm and breadth at base is 5.5 mm. Although the vertebral column posterior to Cd14 is not preserved, from the perspective of diapophyses reduction it may be estimated that the diapophyses terminate at Cd17 or 18. Caudal neural spines are posteriorly inclined and gradually decrease in angle posteriorly. Pre- and postzygopophyses are relatively large with postzygopophyses migrating dorsally toward the neural spine. At Cd13 the postzygopophyses have migrated to the dorsomedial section of the neural spine.

In summary, the anterior 14 caudals of T6001 display posterior morphological variation by becoming thinner and slightly longer, and the diapophyses gradually shorten, migrating from the neural arch to the dorsolateral side of the centrum. The diapophyses may have terminated at Cd17 or 18. The neural spines narrow posteriorly and their angle of inclination progressively decreases posteriorly. Postzygopophyses gradually migrate up the neural spine posteriorly (see Table 5).

Of the four anterior caudals preserved on T6002, two are relatively well preserved, while the other two have damaged neural spines. A medial caudal has a damaged neural spine and diapophyses. Morphologies do not differ distinctly from T6001, but because T6002 specimens are relatively complete and undistorted they more accurately reflect the characteristics of the anterior caudals and thus are necessary to describe. Compared to T6001 the most anterior caudal (Cd2 or 3) is larger, with nearly circular ends. Ventrally there is a very weak longitudinal keel. Diapophyses are long and slightly flattened dorsoventrally. Lenticular in outline, they extend horizontally, and at their center project very slightly posteriorly. The neural arch-centrum suture is

distinct, and the neural canal is small and elliptically shaped. The neural spine is narrow, high, and posteriorly inclined at an approximate 55° angle. Pre- and postzygopophyses are small. The posterior haemal arch surface on the centrum is larger than the anterior surface and appears as an inverted and perfectly rounded triangle. The remaining 3 anterior caudals (see Fig. 13-D) are characteristically similar to the description above, only they have smaller centra and slightly shorter diapophyses. These specimens were recovered as isolated elements but may be interpreted as representing the articulated series Cd2-5 or Cd3-6, based upon characters such as their size, the extremely weak longitudinal keels, and the lengths of diapophyses. T6002 also preserves a single medial caudal that has a small centrum, distinct ventral lamina and extremely weak processes dorsomediolaterally. This element should represent the most terminal, or approaching the most terminal diapophyses.

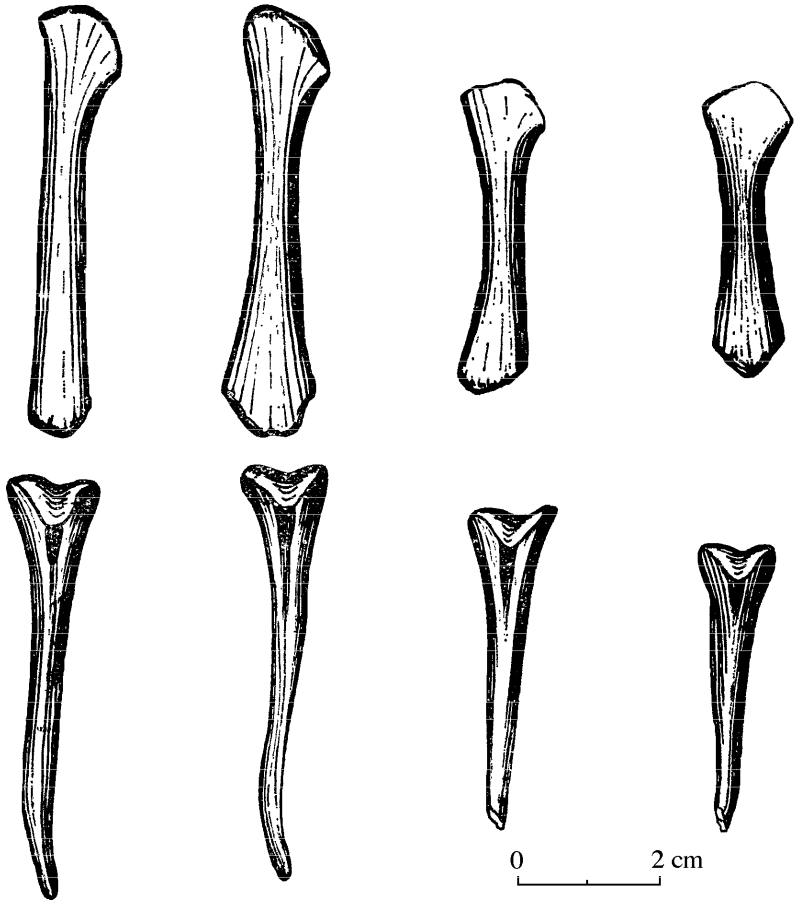

Figure 14. Haemal arches of T6002 *Yandusaurus multidens*.
Upper, lateral; Lower, posterior view. A. Arch 5 or 6; B. Arch 7; C. Mid-caudal haemal arches.

Haemal arches: With the exception of haemel arches 6 and 14 (see Fig. 14, Pl. II-3, Pl. III-1) which are missing, and arches 4-5 which are damaged, the remaining elements are all preserved. They gradually shorten posteriorly, narrowing in anteroposterior breadth from top to bottom while thinning medially to become laterally thin and flat. They are slightly thickened at their center. Dorsal articular surfaces are nearly circular or elliptical and the haemal canal is an elongated oval. A longitudinal trough is present extremely close to the anteroventral canal. Arches 7-13 gradually shorten posteriorly as the shaft thins, medial section constricts, and distal end broadens. Six haemal arches are preserved on specimen T6002. Two represent anterior caudals with elongated arches and nearly circular proximal ends. Other haemel arches anterior and posterior to these are semicircular with a laterally flattened shaft and haemal canal that is an

elongated oval. The other two anterior caudal arches (Fig. 14-A,B) are relatively shortened, and one displays an extremely thin termination that is distinctly broadened anteroposteriorly. These characters strongly resemble arch 7 on T6001. The other two arches (Fig. 14-C, D) are determined to be mid-caudal, or mid to posterior arches.

Ossified tendons: Relatively well preserved ossified tendons are present on T6001 which generally extend longitudinally along both sides of the ventral neural spines. A small number lie on the dorsal spines, and several lie dorsal to the sacral ribs. Their anterior-most occurrence lies at the distal margin of dorsal spine 4, while posteriorly they extend continuously to the first caudal. No interconnected ossified tendons occur posterior to the first caudal, but a relatively short and fine club-shaped piece of bone occurs on the left neural arch of Cd10, which is believed to be an ossified tendon. If this interpretation is correct, then these features would extend at least to caudal vertebra 10.

Ossified tendons on dorsal vertebrae are generally tightly associated on the neural spines in a cross-hatched pattern. The most anterior occurrence is located on the left side at midheight of neural spine D4, where three fine club-shaped pieces taper anteriorly. The left side of the D8 neural spine preserves at least four ossified tendons at midheight and at its base, among which one piece with an elliptical cross-section is located dorsal to the base of the diapophyses. The best-preserved tendons lie on the left side of the D14-15 neural spines, where at least 10 may be observed in cross-section. The most pronounced consists of a broad and flat tendon lying on D15's posterior neural spine where anteriorly it bifurcates into three thin and small branches. This bifurcation phenomenon may also be observed at the dorsal left side of D14's neural spine, where at their point of bifurcation the tendons are laminar but posteriorly they gradually terminate by becoming thin and club shaped. Extremely well-preserved tendons lie on the sacral region (see Pl. I-8) on both sides of the closely spaced neural spines, where at least four strands are arrayed. On the left side more than six may be observed while on the right side several lie distant from the neural spine and are spread out on the sacral ribs. Sacral ossified tendons are all gracile and long. The longest among them reaches over 91 mm and extends anteriorly to the dorsal neural spine of D15, and posteriorly to the spine of S5. On the first sacral neural spine, ossified tendons appear circular or lenticular shaped in cross-section. On the caudal region these tendons are not as well developed as on the dorsal and sacral regions with remnant fragments appearing only on the right diapophysis of C1 and right neural spine of C10.

Table 2. Measurements of cervical vertebrae and cervical ribs on *Yandusaurus multidens* T6001 (mm).

Sequence	Total vertebral height	Length (ventral)	Posterior height	Posterior breadth	Rib length
1					25+
2	31.9	15.5	—	9.5	—
3	26.5	18.7	—	10.1	—
4	25.5+	18.0	—	11.0	17+
5	24.5+	18.0	12.0	11.0	19+
6	27.0	17.4	—	11.6	11+
7	28+	17.0	11.5	12.2	22+
8	28.6+	17.0	—	—	31+
9	30.8+	15.3	—	—	55

Table 3. Measurements of dorsal vertebrae and dorsal ribs on *Yandusaurus multidens* T6001 (mm).

Sequence	Total vertebral height	Length (ventral)	Anterior height	Anterior breadth	Neural spine height (above processes)	Neural spine breadth	Right rib length	
							Linear	Curvature
1	34+	14.5	11.2	—	5.6+	6.8	75	85
2	36.0	14.2	11.0	10+	11.4	7.6	71	81
3	37.0	14.5	11.5	11.5	13.4	8.4	82	91
4	33+	13.5	11.6	11.5	12.0	8.5	62	69
5	—	14.0	—	—	14.0	10.0	50+	50+
6	38.0	14.0	12.0	11.5	15.0	12.3	67	73
7	31+	15.2	12.0	11.9	14.5	11.8+	46+	48+
8	35.0	16.0	12.0	12.6	14.0	14.7	41+	41+
9	34.4	17.0	12.3	13.4	14.5	12.0	30+	30+
10	35.0	17.0	—	13.8	15.2	13.3	45+	45+
11	34.5	17.7	—	14.4	14.2	13.5	34+	37+
12	36.0	17.1	13.0	14.8	15.0	14.5	14+	14+
13	35.0	17.6	13.2	15.0	14.0	15.8	19+	16+
14	35.5	18.0	13.6	15.4	12.2	14.0	26	26
15	34.0	19.0	14.0	16.6	—	—	26	26

Diagnostic characters of *Yandusaurus multidens* ossified tendons include relatively good development in the dorsal and sacral regions. The dorsal region displays an anteroposterior tendency to thicken and increase in number. The tendons are predominantly elliptical in cross-section. Distally they gradually alter to a thin club shape. Many of the tendons run parallel to the neural spines' alignment, that is to say, perpendicular to the spines themselves. Posterior dorsal vertebral tendons are thick, strong and bifurcated, and they intersect with the long sacral tendons in a cross-linked fashion, which would strengthen sacral movment.

Table 4. Measurements of sacral vertebrae on *Yandusaurus multidens* T6001 (mm).

Sequence	Total vertebral height	Length (ventral)	Centrum anterior height	Centrum anterior breadth	Neural spine height (above canal)	Neural spine breadth
1	33.3	20.0	11.5	20.5	16.7	17.5
2	34.0	19.0	11.5	23.5	16.0	20.0
3	35.0	19.0	—	19.4	—	19.0
4	35.0	19.0	—	19.0	—	17.3
5	36.0	17.0	—	18.0	17.0	16.0

Pectoral Girdle and Anterior Limb

Pectoral girdle: T6001 preserves a relatively complete right scapula and corocoid with some minor damage to the distal end. On the left side only the proximal end of the scapula and a fragmentary and distorted corocoid are preserved. A clavicle is not observed nor is a sternum preserved.

Scapula: The entire element is rather broad and short with a relatively straight anterior margin and slightly anteriorly curved posterior margin. The distal end is relatively thin and

distinctly expanded with a conspicuously thickened ventromedial section and an inflated lateral side. The proximal end is distinctly expanded with the anterior and posterior margins of the lateral side maintaining an anteriorly inclined and posteriorly inclined keel respectively. The anterior keel is better developed than the posterior keel. Lying between these two keels is a shallow triangular depression (see Fig. 15-A, B, and Pl. III-3, 4). Medially, the scapula is relatively flat with a swollen ridge at the center of the proximal end. The ventral margin of this ridge is broad and spacious and dorsally it gradually attenuates to disappear at the center of the shaft. The suture surface with the corocoid is relatively straight and nearly rhomboid shaped in outline. The posteromedial section is broadest and it becomes narrower anteriorly. The glenoid is nearly semicircular in outline although the cavity itself is nearly circular (see Table 6).

Table 5. Measurements of caudal vertebrae and heamal arches on *Yandusaurus multidens* T6001 (mm).

Sequence	Total vertebral height	Length (ventral)	Height-breadth			Transverse process (caudal rib) length	Haemal arch length
			Anterior height	Anterior breadth	Posterior height		
1	34.5	17.0	15.0	17.0	—	22+	42.0
2	—	17.0	14.9	—	16.3	20+	44.8
3	—	17.0	14.8	—	16.8	23.0	37.7+
4	—	17.0	14.2	—	—	23.7	17.5+
5	—	18.4	14.8	—	15.0	22.0	8+
6	—	18.5	—	—	—	20.0	—
7	28.3	19.0	13.5	12.2	14.2	19.5	36.0
8	26.0	18.2	11.5	—	13.3	11+	36.0
9	23.0	18.8	11.5	—	12.6	—	34.5
10	22.0	18.0	10.0	—	12.2	13.3	30.0
11	22.0	18.5	10.0	—	11.3	10.6	27.0
12	22.0	19.0	10.4	—	11.2	9.5	24.8
13	22.0	19.5	—	—	11.5	8.5	24.4
14	22.6	21.5	10.2	11.5	11.0	6.5	—

Coracoid: The coracoid is relatively large (see Fig.15-A, Pl. III-4) and consists of a relatively thin plate. Laterally it is relatively flat and smooth, differing from the coracoid of *Yandusaurus hongheensis* which possesses a distinct ridge on the anteroventrolateral region. The anteroposterior breadth is slightly larger than the dorsoventral length, such that it is nearly pentagonal in outline. The coracoid foramen is elliptical in shape, its largest diameter is 5 mm, and it is situated at the midpoint dorsolaterally. The dorsal sutute with the scapula is relatively straight. At its posterior region, very close and ventral to the glenoid cavity, is an extremely weak crescentic depression.

Table 6. Measurements of T6001 *Yandusaurus multidens* pectoral girdle (mm).

	T6001 Right	T6001 Left	T6002 right
Scapula length	80.0	41+	128.0
Greatest proximal breadth of scapula	31.5	—	52.0
Greatest distal breadth of scapula	31.0	—	48.0
Smallest width of scapular shaft	14.3	14.7	20.0
Coracoid dorsoventral length	27.4	—	—
Coracoid greatest anteroposterior breadth	31.0	28+	—

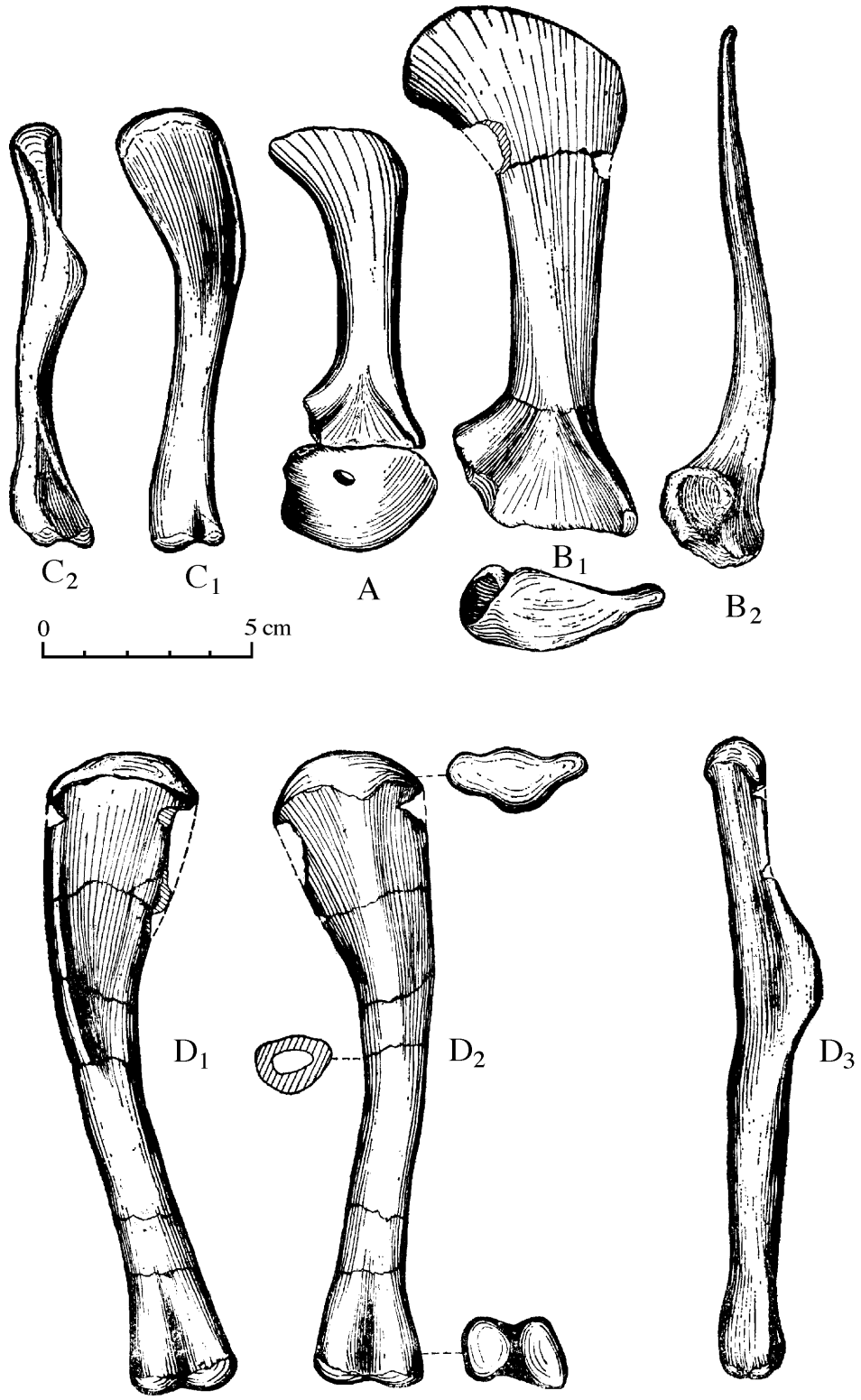

Figure 15. Pectoral girdle and humerus of *Yandusaurus multidens* (x 3/5).A. Lateral view of T6001 right scapula and coracoid; B. Lateral view (B_1) and posterior view (B_2) of T6002 right scapula ; C. Anterior view (C_1) and lateral view (C_2) of T6001 left scapula; D. Anterior view (D_1), posterior view (D_2), and lateral view (D_3) of T6002 right humerus.

Table 7. Measurements of *Yandusaurus multidens* humerus, ulna, and radius (mm).

	Humerus			Ulna			Radius	
	T6001		T6002	T6001		T6002	T6001	
	Left	Right	Right	Left	Right	Left	Left	Right
Length	102.4	101.6	146.7	70	70	95.4	70.0	69.4
Greatest proximal width	22.0	17.6	34+	16.4	13.3	22.0	11.4	10.4
Greatest distal width	15.3	16.9	22.7	—	10.5	17.0	12.7	9.8
Smallest diameter of shaft	6.6	8.5	12.0	—	—	6.5	—	—

Table 8. Metacarpal and phalanx measurements of T6001 *Yandusaurus multidens* (mm).

		Length (ventral)	Proximal width	Distal width
Mc I		15.0		4.6
	I-1	8.4	4.0	3.7
	I-2 (ungual)	8.4	3.0	
Mc-II		20.3	9.5	5.8
	II-1	10.0	5.6	5.0
	II-2	7.3	4.5	4.3
	II-3 (ungual)	3+	3.1	
Mc-III		20	10.2	6.0
	III-1	9.0	5.3	5.0
	III-2	6.0	4.7	4.2
	III-3	5.0	4.0	3.1
	III-4 (ungual)	—	2.9	
Mc-IV		13.6	6.0	4.4
	IV-1	6.0	4.6	3.0
	IV-2 (ungual)?	4.6+	—	
Mc-V		10.4	6.3	4.6
	V-1	5.0	3.0	2+
	V-2 (ungual)	3+	—	

Anterior limb: A relatively well preserved left anterior limb is present on T6001, and only several of the ungual phalanges are missing. The right forelimb lacks all elements distal to the radius-ulna. T6002 preserves only a right humerus and left ulna.

Humerus: The humerus is gracile and long (see Fig. 15-C, D; Pl. III-2, 5) with a distinctly torsioned shaft and relatively well developed deltopectoral crest that terminates just above the midline of the shaft. Both proximal and distal ends are not as conspicuously expanded as on *Yandusaurus hongheensis*. The narrowest point on the shaft is ventromedial. The medial margin of the humerus is distinctly rotated, while the humeral head is located proximomedially and gradually thins to both sides. At the distal end the medial condyle is large and the lateral condyle is small with a weak trochlea (the right humerus of T6001 has a relatively distinct trochlea that extends for a short distance before terminating). The shaft is hollow but has thick walls.

Ulna and radius: Both elements are nearly equivalent in length and are gracile with straight, hollow, and thickly walled shafts (see Table 7). The proximal end of the T6001 ulna is triangular with a weakly developed olecranon. A thick but shallow longitudinal trough lies at the proximolateral side, which becomes narrow ventrally. The distal end is small, and has a

longitudinally elliptical, thick, and shallow depression on the lateral side. In ventral perspective it is slightly pear shaped. The T6002 ulna is distinctly triangularly expanded at its proximal end, but gradually contracts distally. The lateral side of the shaft is flat, semicircular in cross section, and expands distally into an ellipse. The T6001 radius is long and thin with proximal and distal ends both elliptical. In cross-section the center of the shaft is circular (see Fig. 16.)

Carpus: The left limb of T6001 preserves the ulnare, intermedium, and radiale (see Fig. 16). The ulnare articulates with the distal ulna, is almost pentagonal in shape, and is dorsoventrally thin and laminar with a slightly concave ventral surface. The intermedium is situated ventral to the ulnae and radiale, and is medial to the ulnare. It is flat with a slightly convex ventral surface, nearly circular in outline, and its lateral side covers the medial side of the ulnare. One of the carpals articulates with the proximal end of metacarpal (Mc) III, but because Mc IV has been displaced, it lacks a direct connection with any of the carpals. The last carpal is lenticular, circular, and articulates with Mc V.

Manus: The right forelimb of T6001 is completely lost, but the left forelimb is well preserved (see Fig. 16) with relatively complete and undamaged digits and carpals. Among the ungual phalanges, only ungual 1 is in good condition, as unguals 2-3 are damaged and unguals 4-5 have been lost. The digit formula is 2 3 4 2? The formula of digit 4 is questionable due to poor preservation. Mc II and Mc III are longest, nearly equal in length, and have greatly expanded proximal ends, constricted shafts, and expanded distal ends. Both ventrodisal surfaces have a weak longitudinal trough, which causes a projection of the two condyles. The proximoventral surface of Mc III has a somewhat triangular shallow and distinct depression that extends distally to the midpoint of the shaft. Half of the proximal end of Mc II overlies the proximal side of Mc III. Mc IV and Mc V are thin and flat with expanded proximal ends that are weaker than Mc I. The thin nature of these elements may be due to compressional distortion. Mc V is the shortest metacarpal (see Table 8). Mc I is shorter and distinctly more robust than Mc II or Mc III, with a slightly concave ventral surface and a proximal end that is also more weakly expanded than Mc II and III. Proximally the lateral side overlies the medial side of Mc II. Ventral surfaces of all the metacarpals are smooth, glossy, and unstriated.

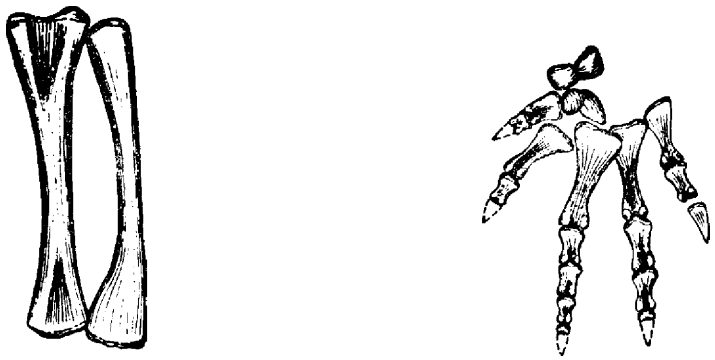

Figure 16. Posterior view of T6001 *Yandusaurus multidens* left ulna, radius, and manus (x 2/3).
R. Radius; U. Ulna; Cap. Carpals, Mc. Metacarpal.

A majority of the phalanges are preserved on digits I-V; however digit IV only preserves one phalanx. The proximal phalanges on digits I and II are rather gracile and long. On digit III the corresponding phalanx is relatively short and robust with a more distinctly curved ventral surface, a slightly flattened posteroventral margin, a thinly constricted medial shaft, and distinctly projected distal condyles. The ventral surfaces of the second phalanges on the second and third digits are quite similar to the proximal phalanges with the only difference lying in their shorter nature and the

posteriorly directed horn-like projection on their posteroventral end, which facilitates the articulation with the medial groove of the proximal phalanx. The third phalanx of the third digit is shorter and smaller than its proximal counterpart, but characteristically similar. The proximal phalanx of digit V is short, small, thin, and flat. Ungual phalanges of digits I, II, and III are clawed, and it is assumed that those on digits IV and V are similar. The ungual on digit I is the largest and is sharply triangular in ventral view. Ventrally it is relatively flat and only slightly curved. Only the proximal ends of the unguals are preserved on digits II and III. These, however are both smaller than the digit I ungual. The distal end of the proximal phalanx on digit V has two well developed condyles with the medial and lateral ligament fossae both preserved, which implies the presence of a second phalanx. In addition, a skeletal impression is present in the matrix near the anterior side of this proximal phalanx. Consequently, it is inferred that the second phalanx of digit V was a clawed ungual.

Pelvic Girdle

Pelvis: T6001 preserves completely paired left and right ilia, ischia, and pubes (see Fig. 17-A, Pl. III-6). T6002 preserves a nearly complete left ilium, right ilium with damaged anterior and posterior ends, and a right prepubic process.

Ilium: Both right and left sides of the T6001 illia are nearly equal in length (see Fig. 17-B, Pl. III-6,7) and both have a thin iliac blade that displays a nearly flat and straight dorsal margin and a relatively flat and smooth lateral side. At the center of the iliac blade there is a very slight medially concave and spacious depression. The dorsal margin of the acetabulum is conspicuously thickened. The anterior iliac lobe is narrow and long with a perfectly rounded termination that is slightly ventrally curved. The anterior lobe of the left ilium is strongly curved anteroventrally due to compressional distortion. A cross-section at the posterior end of the anterior lobe shows a slight medial curve of the ventral margin. The posterior iliac lobe is short and broad with a dorsally thickened dorsal blade. A relatively sharp longitudinal keel lies above the ventral margin and extends to the posterior end and gradually attenuates anteriorly toward the posterodorsal side of the ischiac peduncle. A shallow concave surface lies between the dorsal margin and longitudinal keel. This concave surface is separated from the aforementioned spacious depression at the center of the iliac blade by a broad and gradually swollen projection that extends toward the ischiac peduncle. A distinct longitudinal trough lies between the dorsal and ventral margins; it gradually shallows and attenuates posteriorly. The short and robust pubic peduncle is well developed and triangular in cross-section, with a particularly well developed lateral laminar ridge, but planar medial side.

The right ilium of T6002 is basically well preserved (see Fig. 18-A, Pl. III-8) with a lateral morphology that resembles T6001 and medial characters that supplement the previous description. The posteroventral margin of the anterior iliac lobe is thin and medially curved to form a sharp ridge that extends anteriorly to the center of the lobe and becomes a laminar ridge. A shallow and broad longitudinal depression lies medially between the dorsal and ventral margins of the posterior iliac lobe. The medial side of the left ilium of T6002 preserves distinct sacral costal nodes 2, 3, and 4 (see Fig. 18-B), all of which are thick, uneven, and slightly concave. Node 4 is the largest among the three and nearly elliptical in shape with a transverse projection at its center and a nearly elliptically shaped shallow groove above and below the transverse projection. Node 3 is semicircular in shape with a slightly anteroventrally directed projection at its center. Node 2 is situated near the medial side of the pubic peduncle and is semi-elliptical in shape.

Pubis: This element is thin and long with a sharply pointed anterior end that is composed of a short and thick preprocess. The suture surface for the ilium is nearly oval in outline. The obturator foramen is large, enclosed, nearly elliptical, and directed very slightly anteroventrally. The posterior process is particularly elongated and terminates nearly at the same point as the ischium. The shaft is rotated and elliptical in cross-section at its midpoint. The distal end is thin but very slightly expanded (see Fig. 17-C, Pl. III-6).

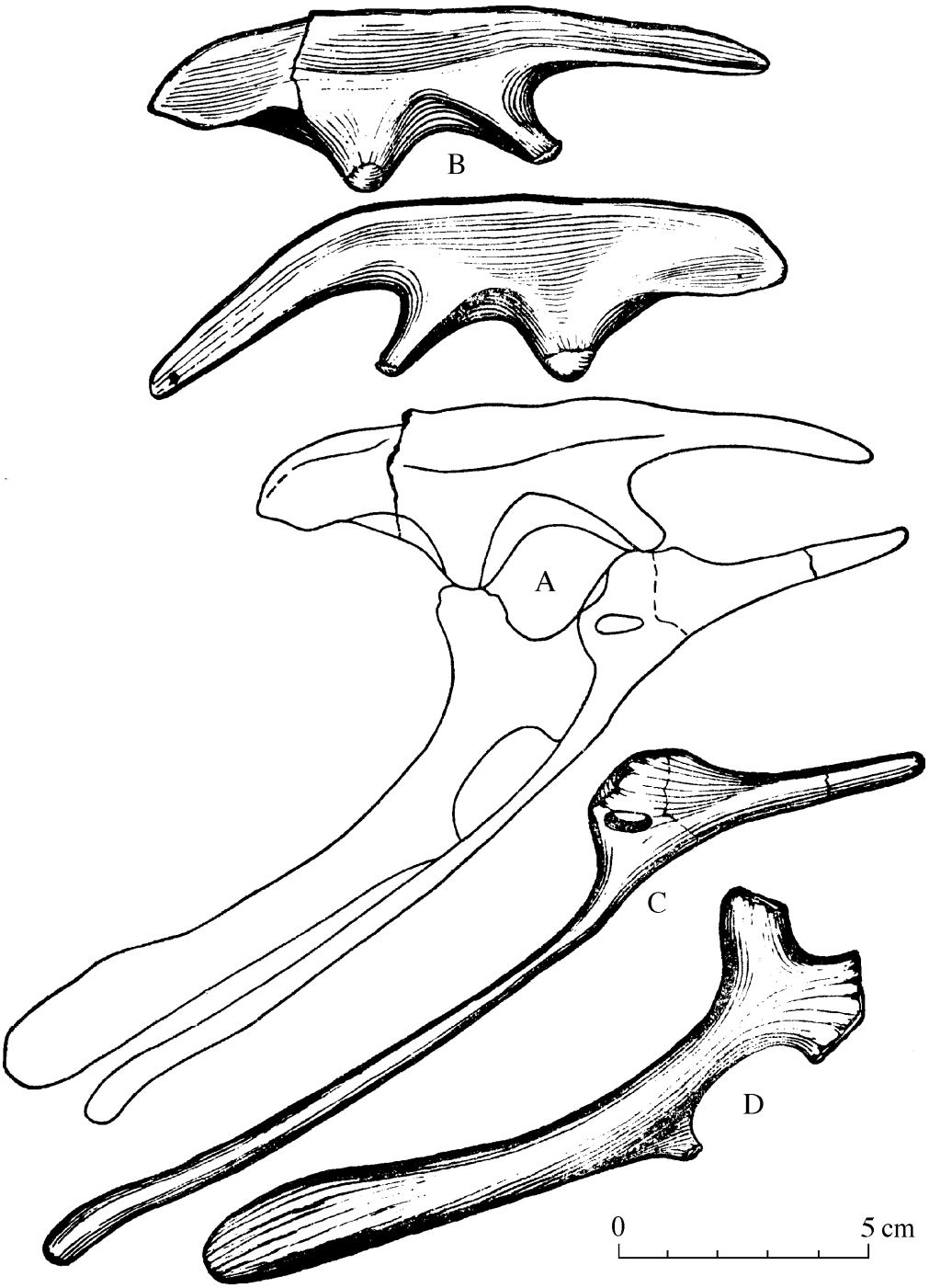

Figure 17. T6001 *Yandusaurus multidens* pelvic girdle (x 2/3).
A. Lateral view of right pelvic girdle; B. Lateral view of left (lower) and right (upper) ilia; C. Lateral view of right pubis; D. Lateral view of right ischium.

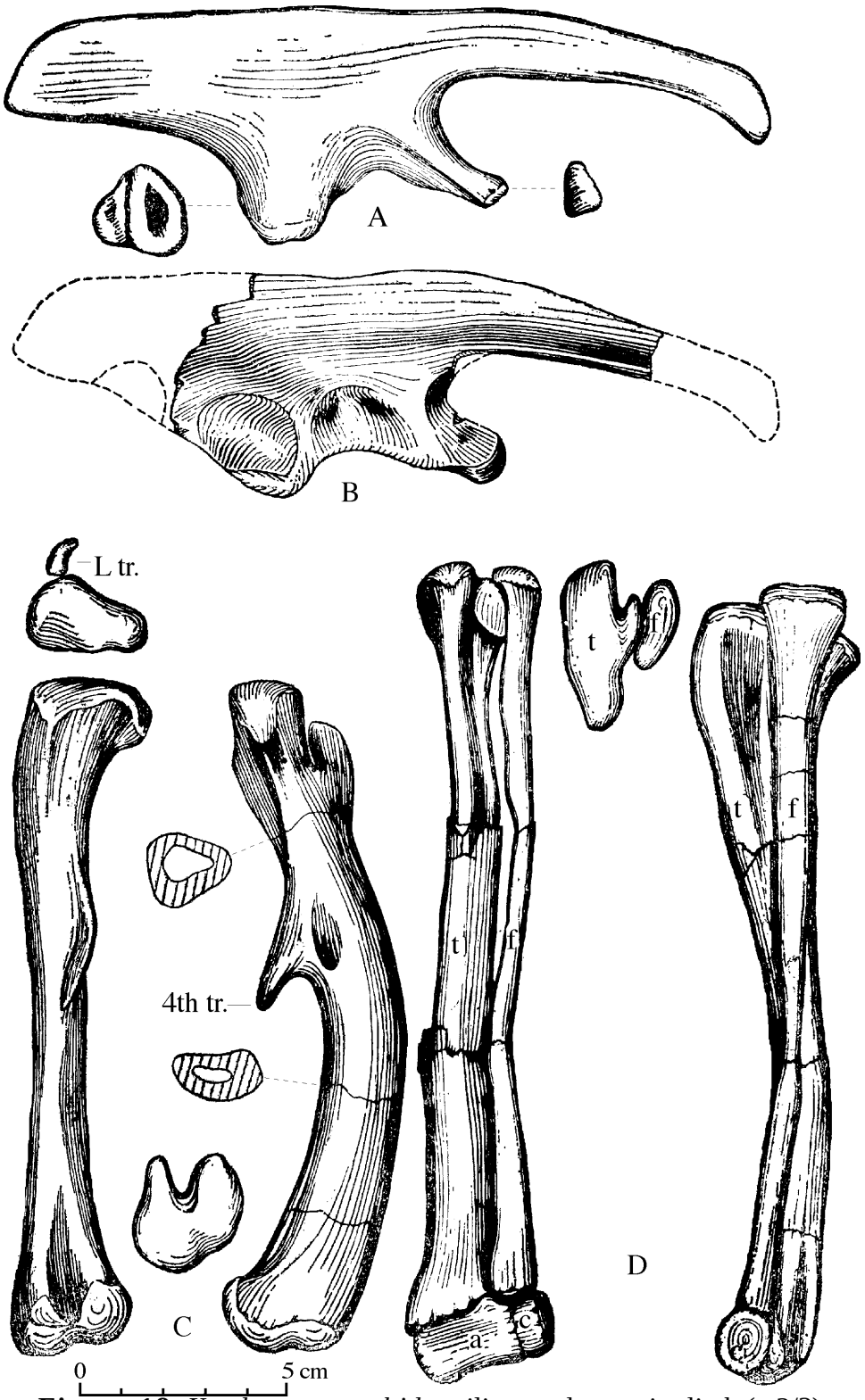

Figure 18. *Yandusaurus multidens* ilium and posterior limb (x 2/3).
A. Lateral view of T6002 right ilium; B. Medial view of T6002 left ilium; C. Posterior view of T6001 left femur (left) and medial view (right); D. T6001 right tibia (t), fibula (f), astragalus (a), and calcaneum (c), anterior view (left), lateral view (right). l. tr. lesser trochanter, 4th. tr. fourth trochanter.

Ischium: Long and broad, this element's proximal end for articulation with the pubis is relatively broad and large. The anterodorsal margin (length 13 mm) is elliptical, smaller than the anteroventral margin (length 15.5 mm), and smaller than the articular surface for the ilium. The obturator process is located proximally, and the shaft is narrowest (9.7 mm) between this process and the proximal end . Distal from the obturator process the shaft gradual broadens, and becomes broadest at the distal end (17.5 mm). At the proximal end, the shaft is relatively thick and gradually thins distally (see Fig. 17-D, Pl. III-6).

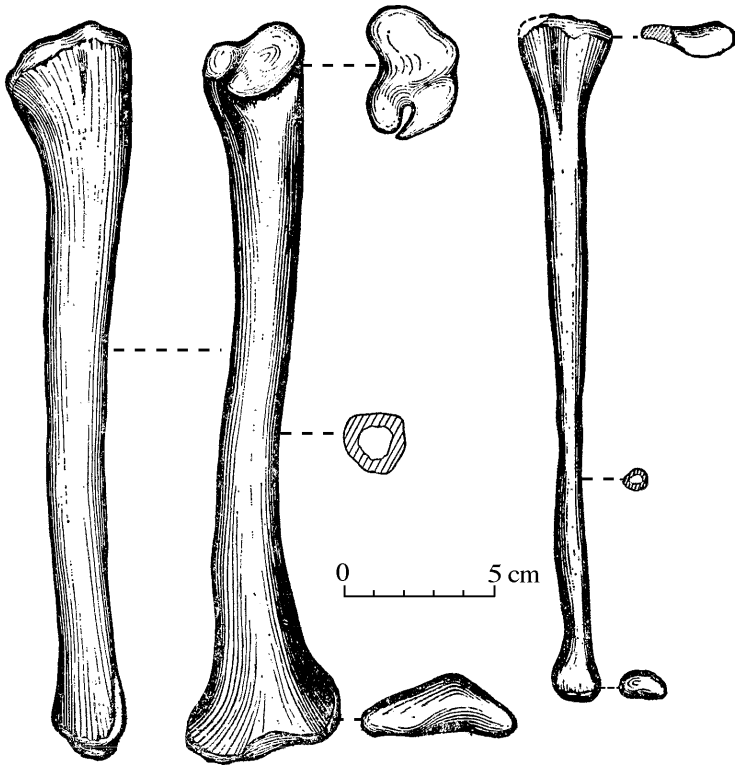

Figure 19. T6002 *Yandusaurus multidens* left tibia and fibula (x 2/5). A. Medial view (left) and posterior view (right); B. Lateral view of fibula.

Table 9. *Yandusaurus multidens* ilium measurements (mm).

	Length	Height	Length of anterior lobe	Proximal height of anterior lobe	Acetabulum breadth
T6001 Right ilium	123.5	23.5	51.0	16.2	31.0
Left ilium	122.0	26.5	50.0	19.0	32.0
T6002 Right ilium	177.0	40.0	71.0	25.5	44.0
Left ilium	116+	40.0	49+	25.5	44.0

T6001 *Yandusaurus multidens* pubis measurements (mm).

	Length	Preprocess length	Postprocess length
Right pubis	188.0	44+	127.3
Left pubis	192.0	58.0	125.7

T6001 *Yandusaurus multidens* ischium measurements (mm).

	Length	Proximal breadth	Distal breadth
Right ischium	136.0	36.0	16.5
Left ischium	135.0	—	—

Hindlimb: T6001 preserves an exceptionally complete left hindlimb, but the right limb has been lost completely. T6002 preserves incomplete left and right femora, left and right tibiae, a left fibula, left and right astragali, and several metatarsals and phalanges.

Femur: The left femur of T6001 is complete, while on T6002 the fourth trochanter is broken and the distal end of the right femur is damaged. Compressional distortion has affected the specimens from the midshaft to the distal end. The shaft is hollow and conspicuously rotated anteriorly (see Fig. 18-C, Pl. IV-1). The anterior end of the greater trochanter is either flat or slightly convex, while laterally it is also slightly convex. The posterodorsal margin has a groove that extends posteroventrally. From a medial view the femur head is slightly trapezoid with a relatively distinct neck lying between it and the greater trochanter. The lesser trochanter is distinctly lower than the proximal articular surface, is mediolaterally compressed, slightly concave medially, relatively broadened and flattened laterally, and is situated nearly perpendicular to the mediolateral axis of the femur head. The fourth trochanter is well developed, typically pendent, and situated proximally on the posteromedial portion of the shaft. Its dorsal margin is sharply blade-like, medially it is flat and straight, laterally it is slightly curved, and the ventral margin is thick. Along the shaft at the medial side of the fourth trochanter lies a thick shallow elliptically shaped groove to facilitate the M. caudifemoralis. The distal end of T6001 has been compressed mediolaterally, while T6002 is compressed anteroposteriorly, but it is still evident that the medial condyle is larger than and slightly more proximal than the lateral condyle. The intercondylar vacuity is relatively wide and deep but an anterior trochlea is absent.

Tibia: The shaft is straight with nearly equally inflated proximal and distal ends. The proximal articular surface is relatively flat, smooth, and slightly inclined laterally. The medial condyle is robust and conspicuously larger than the lateral condyle, which is extended anterolaterally (See Fig. 18-D, Fig. 19-A, Pl. IV-2,3). On T6001 the lateral condyle is clearly flat, thin, and projected slightly posteriorly, but this is the result of compressional distortion. The cnemial crest is slightly larger than the lateral condyle. The proximal sides of the shaft are laterally flattened but rotate anteriorly toward the distal end where they become strongly expanded. On the medial side of the shaft the proximal end is broad and flat, distally it gradually narrows, but again become slightly broadened at its distal end. At its distal end the tibia is a blunt triangle. The articular surface is uneven, and anteriorly near the center there is an open and spacious elliptical depression to facilitate the articulation with the medial swollen ridge and ascending process of the astragalus. Located at the posterior keel of the tibia is a nearly triangular feature for articulation with the posterior sulcus of the astragalus. Anterior and posterior sulci are divided by this ridge. A smooth and nearly elliptical convex surface lies anteroventrally on the lateral condyle to facilitate articulation with the calcaneum. The tibia shaft is hollow with relatively thick walls. Its narrowest point is located at the center of the shaft. In cross-section it is nearly circular. The long axis of the proximal and distal articular surfaces are nearly perpendicular to each other.

Fibula: The left fibula of T6001 is complete, but the proximal end of the left fibula of T6002 is slightly damaged (See Fig. 18-D, 19-B, Pl. IV-2). The element is gracile, straight, and slightly shorter than the tibia (see Table 10). The proximal end is clearly more inflated than the distal end with a relatively smooth and flat articular surface that is slightly inclined medially. From a proximal perspective it is kidney shaped. The articular surface is level with that of the tibia. There is a shallow, longitudinal, and elliptically-shaped convex surface that lies medially on the

proximal end that represents the contact point with the lateral condyle of the tibia. The proximal end of the fibula rapidly constricts ventrally and ventral to the tibial sulcus it is elliptical in cross-section. The shaft is narrowest in its distal one-third, circular in cross section, and ventrally it again gradually increases in thickness.

Table 10. Femur, tibia, and fibula measurements of *Yandusaurus multidens* (mm).

	Femur			Tibia			Fibula	
	T6001	T6002		T6001	T6002		T6001	T6002
	Left	Left	Right	Left	Left	Right	Left	Left
Length	156.0	210.0	161+	184.2	244.0	248.0	170.0	223.0
Greatest proximal width	29.2	46.5	46.0	41.0	44.5	54.0	21.5	31+
Greatest distal width	26.7	50.5	—	35.7	51.5	48.5	11.5	15.2
Smallest diameter of shaft	12.0	13.0	—	13.1	19.5	19.3	5.2	

Tarsus: Preserved on T6001 are the proximal tarsals of the left pes including the astragalus, calcaneum and two distal tarsals. T6002 possesses a complete right astragalus and partially damaged left astragalus.

Astragalus: From a ventral perspective the astragalus is an irregular quadrangle. The anterior side is wider than the posterior side, and medially it is longer than laterally. The ventral surface is smooth, slightly convex, and inclined posteriorly. From an anterior perspective it is somewhat rectangular with a small but distinct ascending process near its lateral side. At its center lies a long and shallow trough. Posteriorly the element is slightly concave. The posterior margin is inclined anterolaterally; its medial surface is flat, smooth, and kidney shaped. The anteromedial section is thick, and anteroposteriorly there is a rather elliptical-shaped shallow depression. Two large fossae lie dorsally which are separated by a mediolateral projection. The medial fossa is large and extends anteromedial-posterolaterally, while the lateral fossa is small. Both articulate with the tibia. The lateral side of the ascending process of the astragalus articulates with the distomedial side of the fibula with an extremely small articular surface (see Pl. III-10, IV-5).

Calcaneum: T6001 preserves a complete calcaneum (see Fig. 18-D, Pl. IV-2, IV-5) that is disc shaped with a circular and slightly concave lateral side. The anterior and ventral surfaces are rectangular with the anterior surface flat and ventral surface slightly convex. Dorsally it is trapezoid and very slightly depressed for the articulation with the fibula. Posteriorly it is a crescentic-shaped, medially inclined depression for articulation with the lateral condyle of the tibia (see Fig. 20-A). In cross-section the medial side is crescentic and attenuates sharply posteroventrally.

Distal tarsus: T6001 preserves complete tarsi 1 and 2 (See Fig. 20-B, Pl. III-9). Tarsal 1 is large, thin, and in dorsal and ventral perspective is a right angle trapezoid. The proximal articular surface is smooth and nearly flat. The medial to posterior margins are slightly depressed. The distal articular surface is predominantly a slightly trapezoid shallow depression which articulates with Mt III. Its medial side consists of an inclined concave surface which resembles a narrow and long right triangle, and which articulates at the center of the lateral side of Mt II. Both of these concave articular surfaces are separated by a ridge. The lateral face possesses three small projections with two small depressions between them that articulate with the medial side of Mt II. The central projection is the largest among them. Tarsus thickness gradually decreases from posterolaterally to anteromedially.

Tarsus 2 is small and massive, and in dorsal view it is slightly convex and nearly pentagonal in shape. It articulates mainly with the calcaneum. The ventral surface is relatively flat, triangular, and articulates with Mt IV. Anteriorly it is slightly concave transversely and resembles

the astragalus in possessing a relatively large fossa at its center. The medial surface is a longitudinally concave rectangle. The posterior surface is a perfectly rounded swollen projection.

Metatarsi and phalanges: T6001 preserves complete left metatarsi and phalanges; however the right pes has been lost completely (see Pl. IV-4). T6002 preserves a portion of the metatarsi and phalanges, including the distal end of left Mt I, the shafts of right Mt II-IV, and a complete Mt III. The remaining proximal ends are all missing. Thirteen phalanges are present (including five complete unguals). Metatarsals I-IV are all hollow.

The first metatarsal (Mt I) is rather well preserved on T6001, being relatively gracile with a flat lateral shaft and curved medial shaft. The proximal end is slightly inflated while the distal end is strongly inflated and triangular in distal perspective. The medial side of the shaft has a small elliptically shaped shallow depression proximally, while distally the shaft has a broad and flattened depression. Laterally there is a broad, large, and rounded shallow fossa. The dorsal surface is sharply angular and is steeply inclined toward the proximal end. At the distal end the ventral surface of the shaft is broad and flat and becomes narrower toward the midpoint. From the midpoint to the proximal end the shaft appears as a laminar ridge. The lateral condyle is distinctly larger than the medial condyle (see Pl. III-11).

Mt II is preserved completely on T6001. It is relatively robust with a thick rectangular proximal end. The articular surface here is slightly flat and the posterolateral margin is laterally inclined where it articulates with the distal end of tarsal 1. The shaft is relatively high and narrow and becomes more gracile distally. The medial side is flat and straight. The distal end is relatively robust and from a distal perspective slightly resembles a constricted trapezoid. The lateral surface has a broad and large shallow depression. The medial surface is broad, flat, and slightly concave. The lateral condyle is large while the medial condyle is small. The intercondylar groove is relatively broad and deep.

The best-preserved Mt III is from T6002 (see Fig. 20-D, Pl. III-12), as the distal end of Mt III on T6001 is missing. Mt III is the largest in the metatarsal series with a nearly rectangular proximal end and a slightly convex medial side. The lateral side of the shaft is flat and straight and at its midpoint is broad and flat. The distal end is robust and resembles a transverse trapezoid. The lateral condyle is slightly larger than the medial condyle and the intercondylar groove is shallow. The lateral side of the distal end is more concave than the medial side. The dorsolateral surface has an anterolaterally extended, elliptically shaped shallow depression.

Only T6001 preserves a complete Mt IV, as that on T6002 lacks its proximal end. The proximal end is a perfectly rounded inflated triangle. The inflated distal end resembles a parallelogram, with the medial side higher than the lateral side. The lateral condyle is slightly weaker and is extended and inclined laterally. A lateral depression is shallow and small (see Fig. 20-C).

Mt V is preserved only on T6001 as a short and small element one-third the length of Mt III. Its proximal end is slightly damaged but from a proximal perspective is elliptical in shape. Distally, the shaft gradually becomes more gracile and appears more wedge shaped. An articular surface is lacking on the distal end. Because of compressional shifting, this element is situated ventrally between Mt II and Mt III.

The left pes of T6001 preserves the complete phalangeal formula of 2 3 4 5 0. With the exception of the proximal end of phalanx III-1 and a portion of ungual phalanx IV-5, all phalanges are complete. T6002 preserves 13 phalanges (see Table 11).

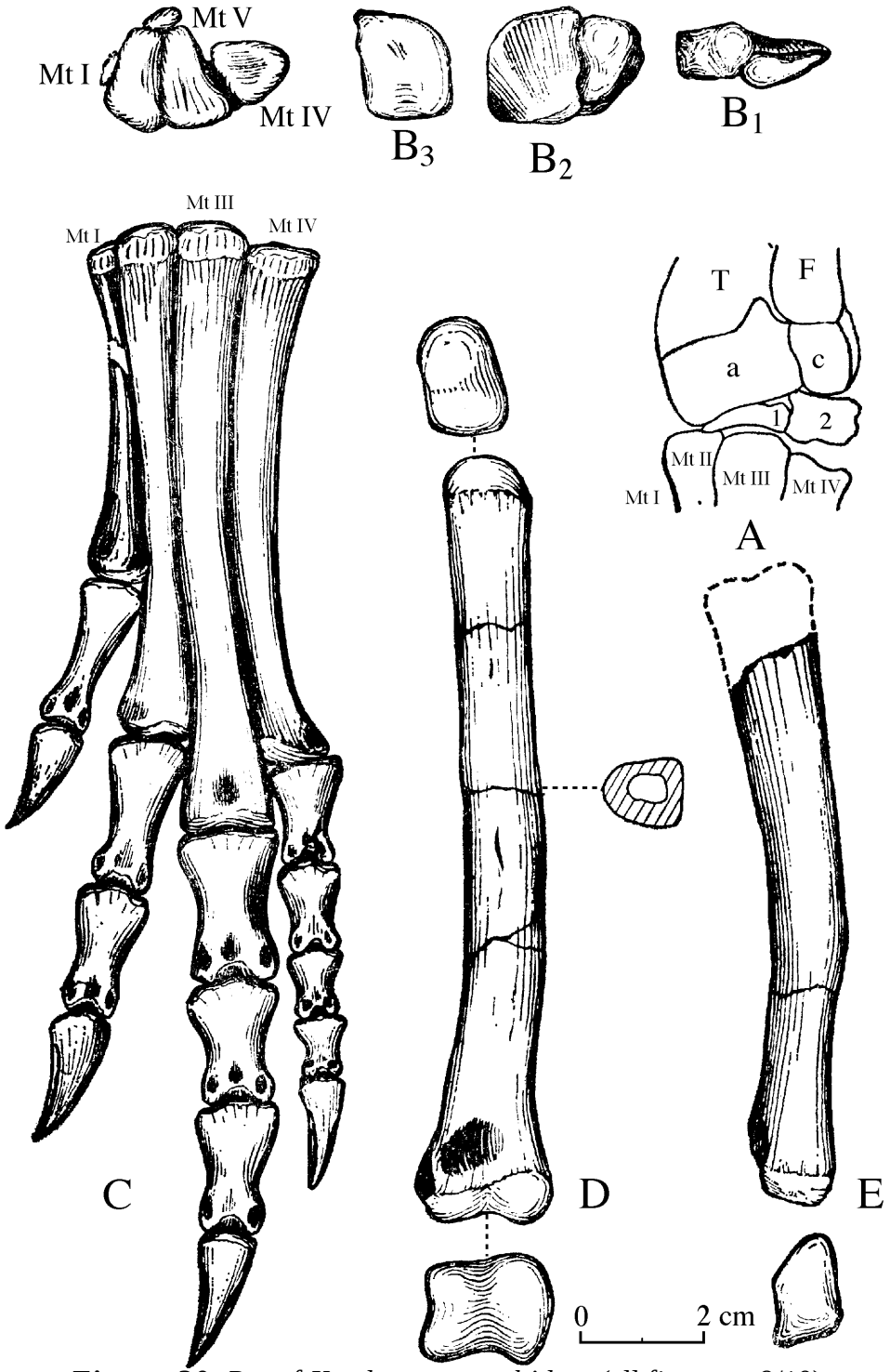

Figure 20. Pes of *Yandusaurus multidens* (all figures x 9/10).
A. Diagrammatic sketch of T6001 anterior view of left tarsus; B. Distal tarsi 1 and 2 (B_1) posterior view, (B_2) ventral view, (B_3) dorsal view of tarsal 1; C. Dorsal view of T6001 left pes; D. Dorsal view of T6002 right metatarsal III; E. Dorsal view of T6002 right metatarsal IV.
Abbreviations: T. tibia; F. fibula; a. astragalus; c. calcaneum; 1, 2. distal tarsals 1 and 2; Mt I-V; metatarsals I-V.

The proximal first phalanx on digit I is gracile and long with slightly expanded proximal and distal ends. The proximal articular surface is slightly concave and shaped like a perfectly rounded isosceles triangle. Distoventrally the shaft is convex while the anteroventral face is broad and flat. The distal end is slightly trapezoid. The medial condyle is smaller and extended slightly more anteriorly than the lateral condyle. Two ligament fossae are round, the lateral being larger than the medial (see Pl. IV-6a).

The ungual phalanx of digit I is relatively gracile, small, and conical in dorsal perspective. It is slightly medially curved, and has a thickened lateral side that gradually thins medially. Anteriorly it is relatively sharp. Both sides display distinct longitudinal grooves, with the medial groove situated lower than the lateral groove. The proximal end is a transverse oval with a weak median ridge, and shallow medial and lateral articular fossae. The ventral surface is relatively flat but posteriorly it is distinctly curved (see Pl. IV-6b).

The most proximal phalanx of digit II (see Pl. IV-7) is relatively robust with a distinctly expanded proximal end that resembles a well rounded isosceles triangle in proximal perspective, and has depressed articular surfaces. The distodorsal surface has a well-developed, longitudinally elliptical depression. The lateral condyle is distinctly larger and more anteriorly extended than the medial condyle. The lateral ligament fossa is distinctly larger than the medial fossa, and the intercondylar groove is relatively broad and deep.

Phalanx 2 on digit II (see Pl. IV-7) is shorter and smaller than the phalanx proximal to it. The proximal end is a well-rounded equilateral triangle with a distinct central ridge and with posteriorly projected angular processes formed on both the dorsal and ventral surfaces. On both sides of the medial ridge are high, narrow, and shallow lateral articular fossae. On the medial side, the fossa is slightly lower, broader, and deeper. The distal end is characteristically similar to the phalanx proximal to it with the only difference lying in the intercondylar surface being a shallow trough.

The ungual phalanx of digit II is morphologically similar to that on digit I but is less recurved and is longer and larger. A relatively well developed central ridge lies on the articular surface. Articular fossae resemble those on digit 2 (see Pl. IV-7,8).

The proximal phalanx of digit III is the largest within the phalangeal series and is robust, relatively broad, and flat (see Pl. IV-4). The shaft is hollow and in cross-section is nearly rectangular. At the distal end the lateral ligament fossa is deeper and slightly larger than the medial fossa. A distinct transversely elliptical depression lies on the dorsal surface.

The second phalanx of digit III is shorter and smaller than the preceding phalanx and more robust than the proximal phalanx of digit II. The proximal end is a well-rounded triangle. Distally, the two condyles and ligament fossae are nearly equivalent in size. The dorsal depression is smaller and deeper than on the preceding phalanx.

The third phalanx of digit III is shorter and smaller than its preceding phalanx and morphologically similar, with the exception of the lateral condyle and ligament fossa being larger than the medial condyle and fossa, and the intercondylar surface is a shallow longitudinal trough.

The ungual phalanx of digit III is the largest among the claws, with an oval proximal end that is slightly concave, bears a distinct medial ridge, and has a lateral articular fossa larger than the medial fossa. The ventral surface is broad and slightly projected medially. On the medial side a longitudinal groove is broader, shallower and situated slightly lower than on the lateral side (see Pl. IV-9).

Table 11. *Yandusaurus multidens* pes measurements (mm).

Astragalus	T6001 Left	T6002 Left	T6002 Right
Anteroposterior length	19.0	24.0	24.0
Medial anteroposterior length	20.0	25.8	25.8
Lateral anteroposterior length	15.3	—	18.0
Anterior breadth	25.0	32.6	34.5
Posterior breadth	18.5	—	25.5
Height (by ascending process)	12.7	—	16.5

T6001 Left	Length	Breadth	Height
Calcaneum	13.4	8.8	16.0
Tarsal 1	6.5	14.8	17.8
Tarsal 2	8.6	11.0	15.0

			Proximal		Distal	
T6001	Left	Length	Breadth	Height	Breadth	Height
Mt-I		51.6	3.0	6.5	8.0	8.5
	I-1	26.3	9.0	8.5	8.1	6.0
	I-2 (ungual)	16.0	7.1	6.4		
Mt-II		83.0	9.0	17.3	12.3	11.4
	II-1	28.0	12.3	12.0	10.3	9.0
	II-2	20.5	10.7	10.2	9.0	7.0
	II-3 (ungual)	23.0	8.4	7.7		
Mt-III		97.5	11.0	17.0	15.6	13.0
	III-1	27.0	16.0	12.5	13.6	9.6
	III-2	19.0	13.0	11.0	11.7	8.2
	III-3	17.3	12.0	9.8	10.0	6.5
	III-4 (ungual)	24.5	8.7	8.0		
Mt-IV		81.6	12.7	12.0	10.0	13.0
	IV-1	18.8	11.2	11.0	10.2	8.7
	IV-2	13.4	10.0	9.8	9.2	7.1
	IV-3	12.0	8.8	7.7	7.7	5.5
	IV-4	10.5	8.2	7.5	7.0	5.5
	IV-5 (ungual)	16±	6.6	—		
MT-V		36.0	3.8	5.0		

The proximal phalanx of digit IV is the shortest, smallest, and broadest among the proximal phalanges (see Pl. IV-10). Its proximal end is slightly concave and shaped as a well-rounded equilateral triangle. Distally the medial condyle is larger than the lateral condyle and is extended ventromedially. The medial ligament fossa is also larger than the lateral fossa and there is a distinct depression on the dorsal surface.

The second and third phalanges of digit IV resemble the preceding phalanx, and differ only by being shorter and smaller. They possess a medial ridge on the proximal articular surfaces and each displays two shallow articular fossae.

The fourth phalanx on digit IV is the smallest within the series and is morphologically similar to the proximal phalanx, with the only difference being a shallow longitudinal trough dorsodistally on the intercondylar surface.

The ungual phalanx of digit IV has been damaged on its lateral side and distal end, but from the portion that is preserved, and based upon the impression left in the matrix, it appears to be equivalent in size to the ungual of digit I.

T6002		Length	Proximal		Distal	
			Breadth	Height	Breadth	Height
Mt-I	(left)	27+	—	—	9.5	15.4
	I-1 (left)	32.3	11.7	10.7	10.5	7.6
	I-2 (left ungual)	26.7	9.0	8.6		
Mt-II	(right)	97+	12.3	—	14.3	15.5
	II-1 (left)	34.0	14.7	15.7	13.0	12.2
	II-2 (left)	25.0	13.8	13.6	11.4	9.0
	II-3 (left ungual)	33.0	10.0	10.4		
	II-2 (right)	24.6	14.2	13.1	12.3	9.0
	II-3 (right ungual)	31.5	10.4	10.7		
Mt-III		120.0	12.8	20.0	20.0	17.0
	III-2 (left)	26.5	17.0	14.0	15.8	10.4
	III-4 (left ungual)	35.4	10.5	11.2		
Mt-IV	(right)	98.7		17.5	12.2	15.4
	IV-2 (left)	25.0	13.8	13.6	11.4	9.0
	IV-2 (right)	24.6	14.2	13.1	12.3	9.0
	IV-4 (right)	11.5+	10.0	8+	9.3	7.0
	IV-5 or I-2 (right ungual)	27.0	8.0	9.0		

Note: Ungual lengths were measured along dorsal curvature.

Comparison of Skeletal Elements

Skeletal lengths of T6001 are as follows (in mm):

Skull	90 (estimate)
9 cervical vertebrae	153
15 dorsal vertebrae	278
5 sacral vertebrae	99.5
14 anterior caudal vertebrae	285
Anterior limb (humerus, ulna, Mc III)	192.4
Posterior limb (femur, tibia, Mt III)	437.7

T6002 preserves only the humerus and ulna, as Mc III is absent, but it is estimated that the length of the anterior limb would be approximately 270 mm. The posterior limb is 574 mm.

Yandusaurus multidens exhibits characters that are attributed to the Hypsilophodontidae, including a small cranial-to-body ratio, relatively large orbits, posterior limb length that greatly exceeds dorsal vertebra length, tibia-fibula are longer than femur, tibia is longer than fibula, Mt III exceeds one-half the length of the femur, fourth trochanter is situated on the proximal half of the femur, and length of posterior limb greatly exceeds the anterior limb (see Table 12). These characters also represent the generalized bipedal and rapid cursorial ornithopod designated by R.A. Thulborn (1977) as the dolichopod model.

III Discussion of *Yandusaurus multidens* Size, Allometry, and Individual Variation

Yandusaurus multidens is the most common small ornithopod from Dashanpu, Zigong. As excavations are still ongoing, the total count of individuals is unknown. Since the initiation of excavations by the Sichuan Zigong Dinosaur Excavation Team in 1981, it is estimated that there have been at least 11 individuals represented. Specimen T6001 still constitutes the best-preserved specimen within the collection, with T6002 being second-best in preservation. Additional individuals are represented by isolated limb bones or vertebrae. T6002 is undoubtedly the largest individual, estimated to be between 1.8 and 2.0 m in length. A subsequent tibia has been excavated that is distinctly larger than T6002 but it is uncertain whether it is assignable to *Yandusaurus.* T6001 has a complete length of approximately 1.4 m, and sets the standard of variation for the genus, as the vast majority of specimens excavated are either equivalent to it or approximate it in size. A small number of specimens clearly represent juveniles, with one tibia merely 70 mm in length, such that the entire individual would be merely 50-60 cm in length. From these data it is evident that *Y. multidens* is a small species, for all individuals in the collection are smaller than *Y. hongheensis* (with a length exceeding 3 m).

Due to the paucity of complete specimens, it is difficult to make more advanced cranial comparisons or to discuss the allometric variation within the species, and hence only several preliminary inquiries may be undertaken here. Perhaps better specimens collected in the future will permit a more comprehensive assessment. The best data for the study of dinosaurian allometry is probably the collection of *Protoceratops.* B. Brown et al. (1940) conducted a study of the morphological and allometric variation with particular emphasis on the cranium, based upon 46 skulls and a large collection of postcrania. Additional studies with similar conclusions were undertaken by H. Osmolska et al. (1972) on *Gallimimus*, and by W.P. Coombs on *Psittacosaurus.* Dinosaurian allometry is becoming an increasingly significant field of study.

Specimen T6001 has exceptionally large orbits, with their length exceeding one-third the length of the skull (or approximately 36%). Additionally, the orbits are situated anteriorly with the distance between the anterior margin of the orbit and the anterior tip of the skull nearly equivalent to the distance between the posterior margin of the orbit and the posterior margin of the skull. The cranium is conspicuously arched dorsally, and the frontals are enlarged to a length nearly 40 percent the length of the skull. Particularly noteworthy is the size of the orbits, which exceeds those of the restoration of *Hypsilophodon* (Galton, 1974), *Dryosaurus altus* (Galton, 1981), and the restoration of *Dysalotosaurus* (Janensch, 1955), as the three latter taxa possess orbits that do not attain one-third the length of their skulls. Moreover, the orbits on *Y. multidens* are also more anteriorly located. Allometric studies of *Protoceratops, Psittacosaurus,* and *Gallimimus* indicate that the size of the orbits gradually decrease in proportion to size, the rostral (antorbital) region of the skull becomes lengthened, and the dorsal cranium gradually flattens with age. Consequently, the characters of T6001 indicate this individual to be a juvenile. Osmolska believed that the allometric changes in the Ornithischia resulted in the anterior to posterior limb ratio being smaller in juveniles. T6001 has a ratio of 44 percent, while on T6002 the ratio is 47 percent, which is further evidence for immaturity. However, it should be noted here that cranial data on *Yandusaurus* are very restricted, as is comparative material, and diagnostic characters for genera within the Hypsilophodontidae include large circular orbits, small skull, and short rostrum. Hence, the preliminary conclusion that T6001 is a juvenile is still hypothetical. A contrasting character suggesting maturity lies in the complete and not partial fusion of sacral vertebrae. Furthermore, the neural arch-centrum suture lines are all very distinct in the cervical, dorsal, and caudal vertebrae of both *Y. hongheensis* and *Y. multidens* specimens T6001 and T6002. This differs from the condition of complete fusion noted on other dinosaurian taxa. Consequently, from these characters it is not possible to conduct age determinations. It appears that data are still too restricted to confirm allometric development within this genus.

IV Skeletal Restoration of *Yandusaurus multidens*

Skeletal reconstruction is primarily based upon T6001. Numerous caudal vertebrae are missing as only 14 caudals are present. At the very least, the caudal vertebral count in the Ornithischia exceeds 40, and generally lies around 45-50. Assuming a minimum count of 40 or slightly more, T6001 should reach an approximate length of 1.4 m. The restored skeleton is reconstructed in an ambulatory posture with the vertebral plane at 40° (see Fig. 33). The tail is inferred to retain a large amount of elasticity due to the lack of well-developed ossified tendons on the distal caudal region. It is very possible that a portion of the distal tail dragged during locomotion. This posture differs from the restoration of *Hypsilophodon* made by Galton (1974). Cervical ribs, dorsal ribs and haemal arches are restored based upon the morphology of the specimen. Dorsal ribs are distinctly small and short, or similar to those of *Dysalotosaurus lettow-vorbecki* (Janensch, 1961). *Yandusaurus* probably had a gracile bipedal body that was nimble in structure with particularly long hindlimbs and short and small forelimbs. It was adapted for rapid cursoriality.

With regard to the skull, a sclerotic ring is absent or perhaps was not ossified. The nares were positioned extremely anteriorly on the rostrum. The mandible of T6001 indicates that a predentary similar to other ornithischian dinosaurs should be present, although no predentaries are represented to date. Articulation of the quadrate with the mandible should have occurred ventral to the plane of mandibular dentition. A clavicle was perhaps absent on the pectoral girdle and the presence of a sternum is not indicated. Due to the complete preservation of the remaining sections of skeleton, serious errors regarding the morphology and size of *Yandusaursus* are not expected.

Section II. Supplementary Description and Comparison of *Yandusaurus hongheensis*

Yandusaurus hongheensis was discovered in January, 1973, during a phase of construction in the vicinity of Jinzihan near Hongheba Dam, southeast of the municipality of Zigong. At that time the Seventh General Reconnaissance Brigade of the Zigong Museum of Salt Industry (currently the Second Geologic Brigade of the Division of Mines) in conjunction with the authors discovered the specimen while monitoring a construction site. The fossil specimen consisting of a single relatively complete skeleton was uncovered, which, with the exception of a single turtle carapace, was found with no other associated specimens. It is extremely regrettable that there was no consultation with specialists during the course of excavation by workers; serious damage was inflicted upon the specimen, causing a disruption to the skeletal sequence. By the time the specimen reached the hands of paleontologists, much had become lost, with the damage all represented by fresh breaks. After as much restoration as possible, the preserved portions of the skeleton are represented by the following: a right maxilla with complete tooth row, jugal, quadrate, and a single lateral pterygoid, five complete cervical vertebrae, by estimation over ten mostly incomplete dorsal vertebrae, five caudal vertebrae, numerous cervical and dorsal ribs, a single haemal arch, relatively well preserved anterior limbs with some damage to the right corocoid, complete left and right scapulae, left coracoid, left and right humeri, and a single radius. Only a portion of the carpals and phalanges are preserved. The sacrum and pelvic girdle were completely lost. Most of the posterior limbs were damaged, with only a small portion of the femura, tibia, fibulae, tarsals, and phalanges represented (see Fig. 21.).

A single manuscript, describing *Y. hongheensis,* was written and submitted to X.J. Zhao, A.L. Sun, X.T. Liu and X.K. Yeh at the Institute of Vertebrate Paleontology and Paleoanthropology for review. Colleague Z.F. Wang photographed the specimens. The authors hereby gratefully acknowledge their enthusiastic support. Subsequently, an extended abstract was published (He, 1979), but due to editorial limitations the bibliography was omitted.

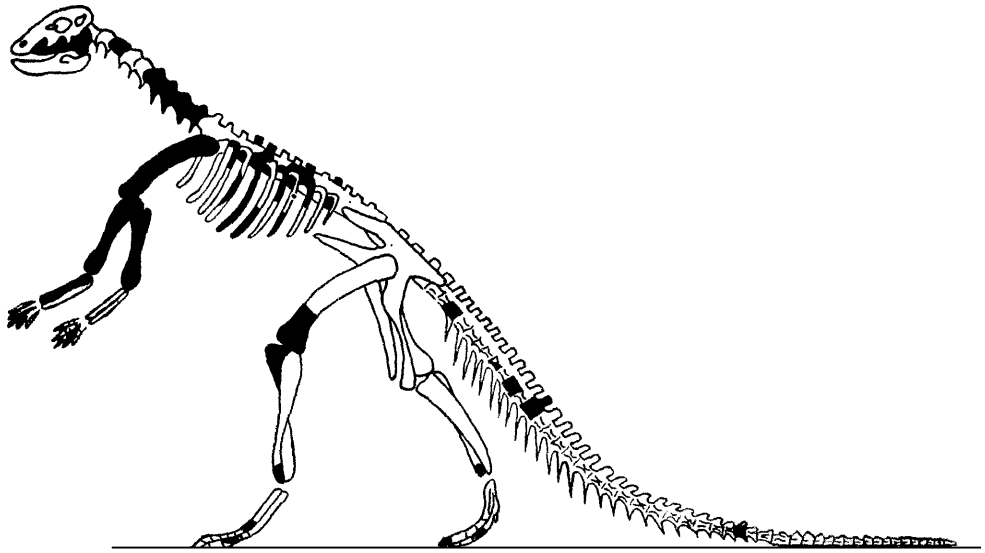

Figure 21. Drawing of preserved bones (in black) of *Yandusaurus hongheensis.*

In 1981, more complete ornithischian dinosaurs were discovered northeast of Zigong from the Middle Jurassic Lower Shaximiao Fm. that underlies the sediments producing *Yandusaurus hongheensis.* These specimens represent *Y. multidens* described earlier in this text. The discovery of these specimens necessitate an in-depth revision of *Y. hongheensis* characters, skeletal structure, and phylogenetic position, in addition to a supplemental description.

I Description

Yandusaurus hongheensis[*] He, 1979

Diagnosis: A relatively large hypsilophodontid with a slightly triangular maxilla containing 15 teeth. A medial keel on the lateral side of the teeth is absent, as only parallel vertical striations are present with an extremely short lateral ridge at the anterior and posterior margins. Cervical vertebrae are platycoelous with a distinct ventral keel and small triangular neural spine. Dorsal vertebrae are amphiplatyan. The scapula is moderate in breadth with a conspicuous swelling at the center of the lateral side. Coracoids are nearly pentagonal in outline with a distinct laminar ridge anteroventrolaterally. The humerus is equivalent in size to the scapula with the posterior margin of the humerus strongly curved as a regular arc. The radius is correspondingly relatively short , being less than two-thirds the length of the femur. The femur lacks an anterior trochlea and the medial condyle is clearly larger than the lateral condyle.

Locality and stratigraphic position: Late Jurassic, Upper Shaximiao Fm., at Hongheba Dam, southeast of Zigong, Sichuan Province.

Skull: Cranial material is represented only by a single relatively complete right maxilla bearing complete dentition, a single left jugal, a single left quadrate, and a single right pterygoid. All these elements were preserved disassociated. A mandible is absent.

Maxilla: Nearly triangular in outline (see Fig. 22, Pl. V-1), this element is more comparable to *Dysalotosaurus* and differs clearly from *Hypsilophodon.* Its preserved length is 112 mm (on the lingual side), but it is estimated to have exceeded 120 mm in total length. The

[*] The initial publication by He and Cai (1983) mistakenly transliterated the species name as *hungheensis* which is hereby rectified.

anterolateral end is broken and there is some slight damage to the posterior end. The ascending lamina is relatively thin, distinctly inclined posteriorly at an approximate 35° angle, and at its highest point is 36 mm above the dental trough. Dorsal to the dental trough 5-8 mm, are four elliptical nutrient foramina that gradually ascend along the maxilla anteroposteriorly. The lingual side of the maxilla becomes distinctly inflated anteroposteriorly. This inflation extends anteriorly to form an anterior process. Dorsomedially there is a thin ascending lamina that seals the antorbital fenestra. This fenestra is bounded by the ascending process and maxillary ramus and is similar in morphology to that on *Y. multidens,* which is an isosceles triangle.

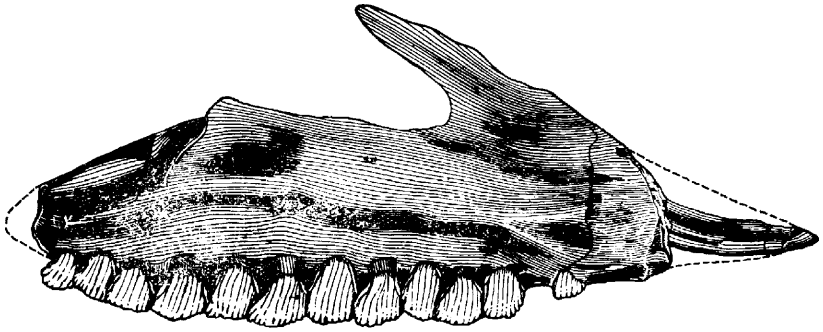

Figure 22: Lateral view of *Yandusaurus hongheensis* right maxilla.

Jugal: This is a left element with some damage anteriorly and posteriorly (see Fig. 23). It is composed of anterior, medial, and posterior processes. It is 82 mm in length. The distance in a direct line from the anterior process to the medial process is 53 mm. The anterior process is relatively broad while the medial and posterior processes are thin and relatively slender. The ventral margin is ventrally curved, which differs from the jugal on *Y. multidens,* which is basically horizontal. A broadened arc is also formed between the anterior and medial process, which should represent the ventral margin of the orbit. It may be inferred from this feature that the orbits are relatively large.

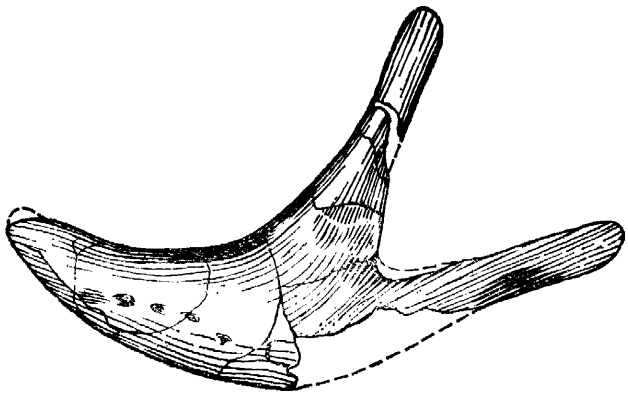

Figure 23. Lateral view of *Yandusaurus hongheensis* left jugal (x 1).

Ectopterygoid: This is extremely well preserved and very closely resembles those on *Hypsilophodon* and *Dysalotosaurus*. In cross-section the peduncle is slightly triangular. Dorsally there is a curved or arc-shaped ridge that extends from the anterior end of the peduncle to the posterior end of the ectopterygoid. Posteromedially a thin and relatively broad lamina extends medially from this ridge. The anteroposterior length is 33 mm and the broadest point at its midpoint is 18 mm.

Quadrate: A single left element is present (see Fig. 24) with a damage occurring on the anterior end and the end for articulation with the dentary. Preserved length is 64 mm. It is triangular in outline, which is similar to *Hypsilophodon*. The posterior end is slightly curved anteriorly. Dorsally, the element is thin, relatively sharp, and triangular in cross-section. Laterally and at its center there lies a semi-elliptically shaped depression which is estimated to exceed 40 percent the height of the entire quadrate and presumed to facilitate the attachment of the dorsally situated quadratojugal. This feature indicates that the quadratojugal of *Y. hongheensis* is quite different from the narrow and long element of *Y. multidens*. Comparatively, the corresponding element on *Hypsilophodon* is larger and morphologically different, although the *Y. hongheensis* quadratojugal is proportionally larger than those on *Dysalotosaurus*, *Iguanodon* and *Champsosaurus*.

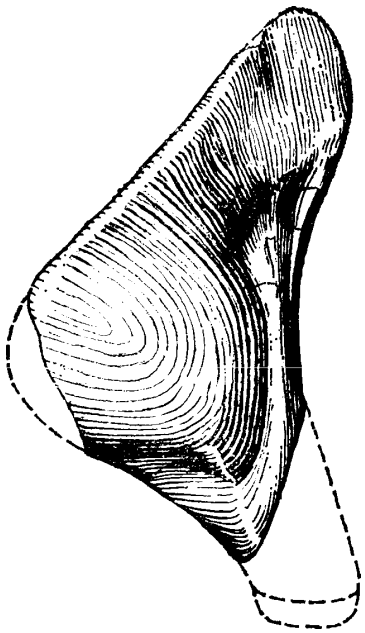

Figure 24. Lateral view of *Yandusaurus hongheensis* left quadrate (x 1).

The specimens preserved are too inadequate to attempt a cranial reconstruction, although they still allow the recognition of certain characters. The length of the maxilla suggests a general estimation of cranial length to exceed 200 mm. The morphology of the jugal implies a relatively large orbit and relatively large supratemporal fenestra with a constricted ventral margin. The short and broad quadrate is moderate in size.

Maxillary dentition: The dentition of *Yandusaurus hongheensis* differs markedly from all other comparable taxa and was recognized as a prominent character for the erection of its genus in 1979. A relatively complete right maxilla is present, containing 12 erupted teeth, to form an extremely well organized 78 mm long dental battery (see Fig. 22, Pl. V-I). The alveolae for replacement teeth suggest that the entire maxilla contained 15 teeth and attained a length of approximately 86 mm. Amongst the twelve erupted teeth, two alveolae lie most anteriorly with one of them containing an newly erupting tooth on the medial side. Medial to the diastema between the first and second erupted teeth lies another alveolus. Therefore, there are three unerupted teeth anteriorly that may be added to the erupted dentition for a total of 15. This state was overlooked in the 1979 description. With the exception of the 3 mm diastema between the first and second erupted teeth, the remaining teeth all lie imbricated with their posterior ends overlapping the anterior side of the succeeding teeth. Several medial teeth are the largest in the series and also display the largest surfaces of imbrication. Anterior and posterior to the medial teeth there is a gradual diminishment in size (see Table 13).

Enamel occurs upon both sides of the teeth. Occasionally, the enamel on the lateral side is a bit thicker than the enamel on the lingual side. There are distinct differences between the lingual and labial sides of the tooth crown, for the labial side is shovel shaped and the lingual side is fan shaped. In addition, the labial sides are all distinctly higher than the lingual sides. This is particularly noticeable among several medial teeth (see Table 13). The tooth margins are serrated, or possess extremely short denticles on the labial side, being approximately 1 mm in length. The denticles extend deeper on the lingual side, become thinner as they extend toward the tooth base, and form into vertical striations that all gradually attenuate before reaching the base of the tooth. The anterior and posterior margins of each tooth possess an extremely short (not exceeding 2 mm) but conspicuous lateral ridge, although on a majority of the teeth an anterolingual and posterolingual lateral ridge is not clear; on a few of the teeth an anterolingual ridge may still be identified. The lateral sides of the teeth are all covered with delicate and vertical parallel striations numbering 7-9. Occasionally, these striations are bifurcated and their thicknesses are relatively consistent. Some extend to the base of the tooth while others become vague upon approaching the

base. A lateral median keel is absent on all the teeth (see Fig. 22, Pl. V-1). Lingually a median keel is also absent regardless of the degree of occlusal wear; however, on the top and in the center of the replacement teeth a faint median keel may be distinguished that does not extend very far toward the tooth base before disappearing. Lingual and labial cingula are absent on all teeth.

Table 13. *Yandusaurus hongheensis* maxillary dental measurements. (Crown height derived from unworn or very lightly worn teeth.)

Dental sequence	Crown breadth (labial side)	Crown height	
		Labial	Lingual
1	4.5	—	—
2	6.0	—	—
3	6.5	8.5	6.0
4	6.5	9.0	7.0
5	7.3	10.0	7.0
6	7.4	11.0	7.0
7	7.4	9.7	6.5
8	7.3	10.0	6.5
9	7.0	—	—
10	7.0	—	—
11	6.0	7.0	5.5
12	4.2	—	—

Two styles of lingual occlusal wear are present, with both consisting of single wear facets in alternate alignment. Relatively distinct, anteroventrally inclined, flat, and lenticular or linear wear facets occur on teeth 3, 5, 7, and 9 (see Fig. 25). Teeth 6 and 8 display a second style that resembles a spatulately concave trough situated medially at the apex of the teeth, and that is much smaller than the previous type. These two facet shapes are well differentiated.

Six replacement teeth are noted erupting beneath the functional dentition. With the exception of the most anterior and posterior replacement teeth, the remaining four occur beneath the more seriously worn teeth with linear facets.

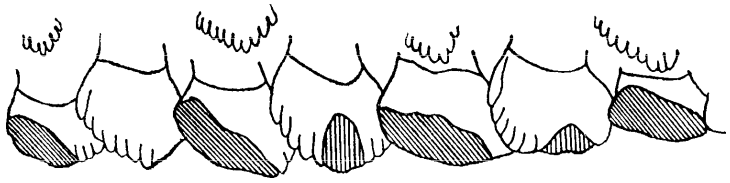

Figure 25. Schematic drawing of lingual wear facets on the maxillary dentition of *Yandusaurus hongheensis* (x 2).

Cervical vertebrae and ribs: Five complete cervical vertebrae are preserved but the atlas and axis are not among them, and the sequence in which they occurred was lost at the time of their collection. After preparation, a gradual morphologic transformation was recognized and it became possible to articulate four of the specimens (see Pl. V-3). Although it is not possible to articulate the remaining fifth vertebra it is evident that it represents the most anterior among those preserved. The cervical vertebral count of *Y. hongheensis* is unknown, but the morphology of the most posterior cervical approaches that of the most anterior dorsal vertebra, and consequently it is inferred that the four articulated cervicals represent the most posterior in the series. Primitive ornithischians within the Hypsilophodontidae generally maintain nine cervical vertebrae, as does *Y. multidens;* consequently, the count for *Y. hongheensis* is provisionally recognized as nine.

Y. multidens has an extremely well developed ventral keel, beginning on Cv4, that persists to the most posterior cervical, while anterior to Cv4 this keel is absent. Through this comparison, the posterior four articulated vertebrae of *Y. hongheensis* may be recognized as Cv6-9, with the more anterior cervical recognized as Cv4, due to the presence of a ventral keel. The absence of Cv5 is recognized by the inability to articulate Cv4 with Cv6.

Cv4: The centrum is relatively gracile and long with a flat anterior end and nearly flat posterior end. It is the longest cervical with the smallest diameter of those preserved (see Fig. 26-A). The centrum is distinctly constricted at its center and a ventral keel conspicuously extends from the anterior to posterior end. The anterior end is narrow (6.5 mm) while the posterior end is broad (13.0 mm). Delicate crenelated striations exist on the centrum anterolaterally and ventrally, but posteriorly the centrum is relatively smooth. Paraphophyses are situated anterodorsally. The neural canal is large and slightly heart shaped. A relatively distinct suture lies at the neural canal-centrum contact which traverses the center of the parapophysis anteriorly. Diapophyses are short and distinctly dorsally inclined. The ventral angle between the vertical axis and diapophyses is approximately 130°. The left and right diapophyses are not symmetrical, as the right side is more ventrally inclined, which is probably due to preservational conditions such as post-burial compression. Prezygopophyses are distinctly lower and have a noticeably broader distance between them than the postzygopophyses. Prezygopophyseal articular surfaces are dorsomedially inclined with anteroposterior diameters of 18 mm and dorsoventral diameters of 13 mm. The neural spine is small with some slight damage at its apex. It may share the same morphology as Cv8, which is slightly triangular in outline.

CV6: Numerous characters of this cervical resemble the previous cervical, such as the centrum outline, size, length, short and dorsally inclined diapophyses, small neural spine, and morphology of the neural canal. Discrepancies include a slightly increased centrum diameter and smaller external angle between diapophyses and vertical axis (approximately 100°). The condition of the ventral keel is opposite to that on the previous centrum, as it has a broad anterior end of 13.3 mm and narrow posterior end of 9.2 mm, and extends directly to the most posterior end of the centrum. Posteroventrally the centrum displays relatively thick crenelated striations.

Cv7: Slight damage has occurred on the dorsal portion of the right zygopophysis at the neural spine, while distinct breakage has occurred on the left diapophysis and left posterior side of the centrum. The rest of the vertebra is well preserved. Its main characters are extremely close to Cv6, and differences lie only in the horizontal extension of diapophyses, being 90° to the vertical axis, a slight increase in centrum diameter, and a slight reduction of centrum length.

Cv8: This vertebra is relatively completely preserved (see Fig. 26-B). Characters including the centrum outline, position of parapophyses, and relative heights of the pre- and postzygopophyses generally resemble the cervical anterior to it. The principle differences lie in slight lengthening and diapophyses inclined at an almost 70° angle to the vertical axis, a nearly rounded neural canal, and enlarged pre- and postzygopophyseal articular surfaces that are nearly round and 20 mm in diameter. The length of the centrum is shorter than Cv7, and the ventral keel has an anterior width of 10 mm, narrows at the center of the centrum, and at the posterior end becomes lost.

Cv9: This specimen is basically completely preserved, with an even shorter centrum, or shortest within the series, and a ventral keel that is generally similar to the anterior cervical but which has lost its lateral laminae and is clearly more rounded. Although the positions of the parapophyses are generally equivalent to the anterior cervicals, there is a trend to shift posterodorsally. Diapophyses are noticeably extended and inclined with a 60° angle to the vertical axis. Left and right diapophyses are not symmetrical, with the right side slightly smaller and shorter. The outline of the neural spine is equivalent to those anterior to it, only it is increased in breadth. The neural canal is slightly expanded.

Table 14. *Yandusaurus hongheensis* cervical vertebrae measurements (mm).

	Cv4	Cv6	Cv7	Cv8	Cv9
Centrum length	50	50	48	46	43
Centrum anterior breadth	26	27	31	28	33
Centrum anterior height	26	23	31	33	34
Centrum posterior breadth	24	34	33	34	37
Centrum posterior height	25	26	28	32	33
Neural canal anterior breadth	17	17	17	16	16
Neural canal anterior height	15	12	12	13	16
Angle of diapophyses to vertical axis	~130° (average)	~100° (average)	~90°	~70°	~60°
Distance between diapophyses	37	48	~55	63	76
Distance between prezygopophyses	30	31	32+	34	39
Distance between postzygopophyses	24	28	28	31	31

The descriptions above and the measurements presented in Table 14 indicate an extremely regular morphologic transformation between Cv4-9, with a gradual tendency to shorten the centrum anteroposteriorly, but conversely with a tendency to gradually increase in diameter. All vertebrae display a flat anterior end and very slightly concave posterior end. Well-developed ventral keels lie on all centra, although there is a trend toward reduction posteriorly. The most noticeable transformation lies in the external angle of diapophyseal inclination which gradually declines from 130° to approximately 60°. The neural spine is small, triangular in outline, and broadens posteriorly. The distances between articular surfaces on the pre- and postzygopophyses tend to increase.

Cervical ribs: Only two complete cervical ribs are present from the right side. One is relatively short (see Fig. 27-A) and corresponds to Cv7, with a projected capitulum that is slightly larger than the tuberculum and an extremely thin and flattened tuberculum and shaft. A well-developed ridge lies on the proximolateral side of the shaft while a corresponding groove lies in the center of the proximomedial side. Its length is 66 mm, capitulum length (from point of bifurcation) is 21 mm, and tuberculum length is 14 mm. A relatively large cervical rib that corresponds to Cv8 (see Fig. 27-B) has a thin and flat tuberculum, shaft, and capitulum. The shaft, however, is proportionally thicker, the capitulum is 25 mm long, and the tuberculum is 14 mm long, which is proportionally shorter than the previous rib. The articular facet is triangular and the entire element is 120 mm. Tubercula of both ribs are broader and flatter than the capitula.

Dorsal vertebrae and ribs: A vast majority of the material is rather fragmentary as there is only a single complete dorsal, five centra, and seven dorsal portions. In total there are portions of over 10 dorsal vertebrae. The sequential order is unknown although the material does allow some observations regarding general characteristics and patterns of variation.

Three specimens are determined to be anterior dorsals; however, they consist only of the dorsal portions of the vertebrae with one being relatively indicative (see Fig. 27-C). The pre- and postzygopophyses are extremely broad with large articular surfaces (anteroposterior diameter of 17 mm and anterodorsal diameter of 19 mm), which are rather similar to the morphology on the posterior cervicals. The majority of posterior dorsals differ in their relatively small articular surfaces. The position of the parapophyses differs from the cervicals by migrating from the anterolateral sides of the centrum to the ventral initiation point on the diapophyses, which represents the lowest point of the parapophyses in the dorsal series. The breadth of the base of the diapophyses is narrower compared to the majority of posterior dorsal vertebrae but broader than on

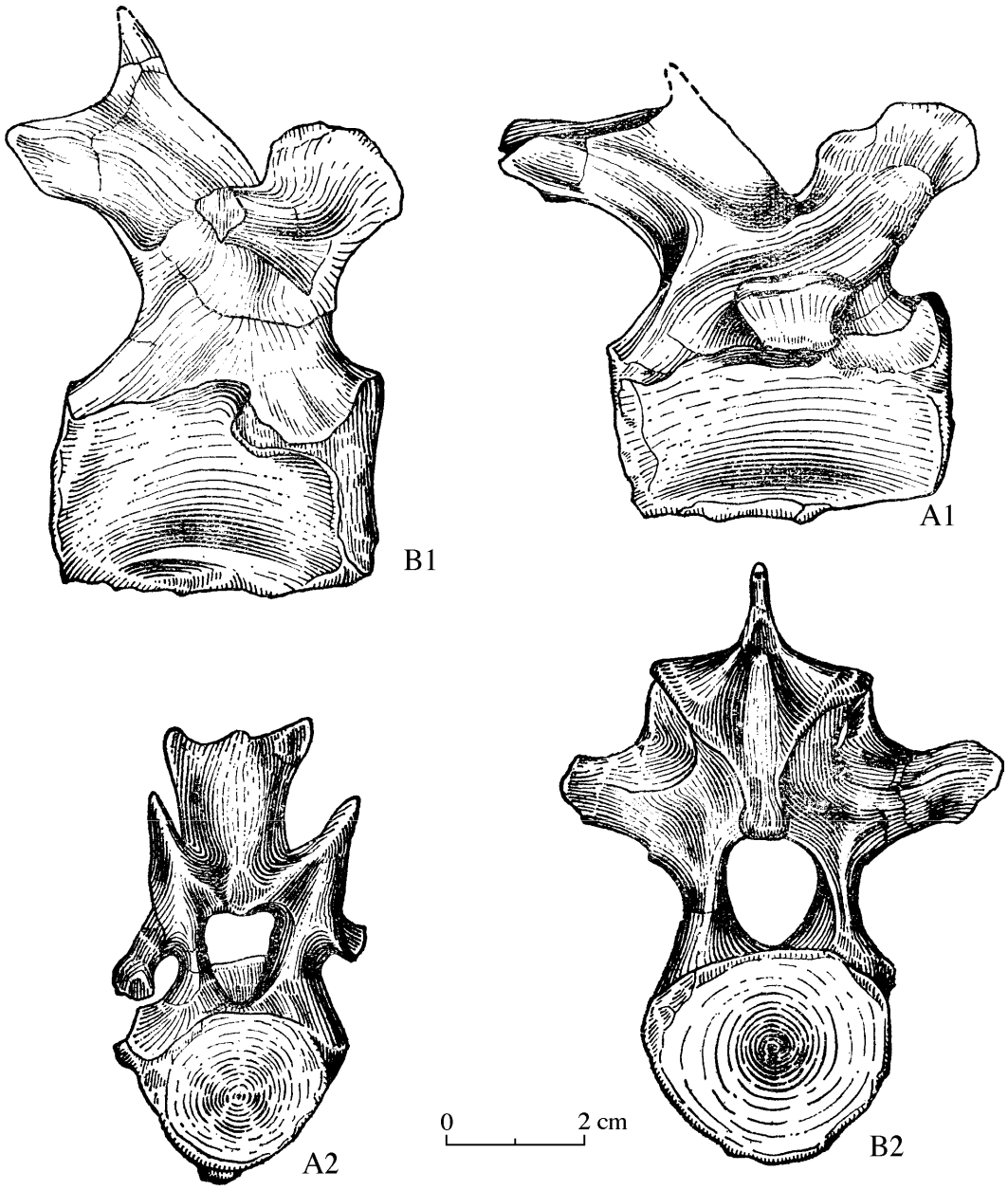

Figure 26. Cervical vertebrae of *Yandusaurus hongheensis* (x 1). A. Cv4: A_1. Right lateral view; A_2. Anterior view; B. Cv8: B_1. Left lateral view; B_2. Anterior view.

the cervicals. The neural spine is damaged, but at the base of the breakage it is 19 mm wide, or distinctly wider than on the cervical vertebrae, but narrower than succeeding vertebrae. The size of the neural canal also lies between the two with a transverse diameter of 13 mm. These features all suggest transitional characters from cervical to dorsal, although there is no doubt that this is a dorsal vertebra. Consequently, this vertebra is recognized as being a relatively anterior dorsal.

Among the dorsal vertebral material there is one complete and undamaged specimen (see Fig. 27-D, Pl. V-2) that, despite exhibiting varying degrees of dissimilarity, compared to the other material, may still represent the generalized condition for *Yandusaurus* dorsal vertebrae. The posterior end of the centrum is flat but the anterior end is very slightly concave, or more nearly amphiplatyan. Laterally, it is slightly flattened with a slight constriction at its midpoint, and it is longer dorsally than ventrally. A suture with the neural spine is distinct and the neural canal is small and nearly circular. The prezygopophyses are short and small, with articular facets that are 13 mm in diameter dorsoventrally, 9 mm in diameter anteroposteriorly, and inclined dorsomedially at an approximate 45° angle. The postzygopophyses are situated slightly higher than the prezygopophyses. Diapophyses are relatively short compared to others in the dorsal series and are inclined at approximately 50° to the vertical axis. The basal section of the diapophyses is broad and triangular in dorsal perspective. Parapophyses with circular facets lie anteriorly and at the approximate midpoint of the diapophyses to form shallow fossae. The neural spine is thin, dorsally extended, relatively broad at its base, and maintains its breadth dorsally to generally form a rectangle that is higher than broad. Measurements are as follows:

Centrum length (dorsally)	42 mm
Centrum length (ventrally)	37 mm
Centrum anterior height	34 mm
Centrum anterior breadth	31 mm
Neural spine basal breadth	34 mm
Neural spine midpoint and dorsal breadth	24-25 mm
Neural spine height	47 mm
Neural spine anterior diameter	12 mm

Compared to the dorsal series on *Y. multidens* this vertebra should represent either a medial or posteromedial dorsal. In addition, there is a single left dorsal diapophysis (see Fig. 27-E) that is extremely short, 21 mm in length, 19 mm in breadth at its distal end and distinctly lacking a parapophysis. An elliptically shaped undulating pit lies dorsally on the diapophysis and represents a rib articulation surface. It is inferred that this is the diapophysis for either the most posterior or second to posterior dorsal vertebra, for this morphology is noted on several species at this position, including *Y. multidens* and *Hypsilophodon foxii.*

Several generalized characters of *Yandusaurus hongheensis* may be determined from the measurements and analysis of preserved material: Dorsal centra are basically amphiplatyan with very little variation in length, being between 42-45 mm, but centra diameters display relatively large variation between 24-37 mm. Ventrally, the centra are smooth and rounded or display a very weak lamina and lack a ventral keel such as noted on the cervical vertebra. All centra display crenulated striations antero- and posterolaterally. Neural spines are all thin plates and may be rectangular. The neural canal is distinctly smaller than on the cervical vertebrae and is generally circular. Parapophyses and diapophyses display relatively large morphological changes. The diapophyses that are represented are all dorsally inclined and vary greatly in length. Anterior dorsal diapophyses are narrow at their base, and long in nature, but become triangularly shaped medially or posteromedially, and finally most posteriorly become short and robust with proximal and distal ends that display no variation. Variations of the parapophyses are principally noted by the gradual migration from the ventral side of the base of the diapophyses to the distal ends. When they reach the anterior midpoint of the diapophyses, it appears that they do not migrate any further distally. On at least one posterior dorsal the parapophyses have become lost. Prezygopophyses on the anterior dorsals are broadly expanded laterally with large articular surfaces, being very similar to those on the cervical vertebrae. Posteriorly these features become relatively short and small and diminish in breadth. The dorsal vertebral count is unknown, but *Y. multidens* possesses 15 and other primitive ornithopods possess 15 to 16. Consequently, it is assumed that *Y. hongheensis* maintains an equivalent count.

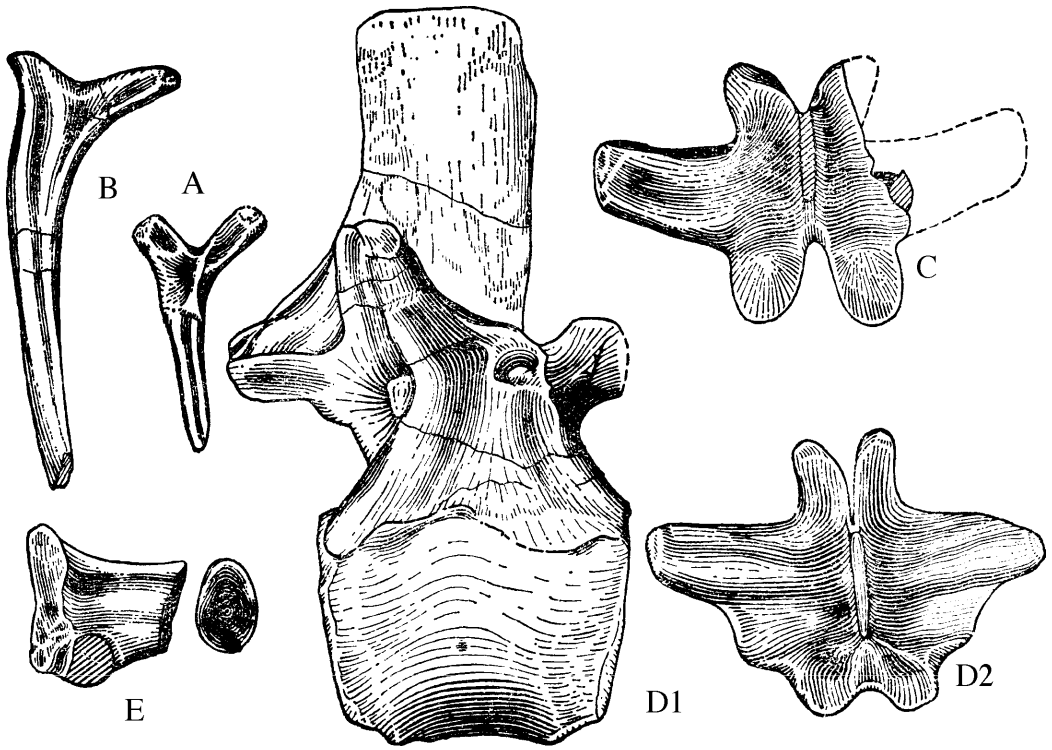

Figure 27. Cervical ribs and dorsal vertebrae of *Yandusaurus hongheensis*. A. Lateral view of right cervical rib 7 (x 1/2); B. Lateral view of right cervical rib 8 (x 1/2); C. Dorsal view of anterior dorsal vertebra (x 2/3); D. Medial dorsal vertebra; D_1. Right lateral view (x 1); D_2. Dorsal view (x 2/3); E. Dorsal diapophysis 14 or 15 (x 2/3).

Dorsal ribs: There are at least 15 to 16 dorsal ribs preserved but many are incomplete. The most anterior ribs are relatively broad, thin, and flat at the anterior end of the shaft, or similar to the posterior cervical ribs, but with a shorter tuberculum. Posteriorly, the proximal shafts become semicircular to nearly circular at their proximal ends, while distally they gradually become thin and flattened. Tubercula represented are all very short. The longest dorsal rib in the collection exceeds 220 mm (see Pl. VI-4, 5). From the perspective of the diapophyses, there is at least one dorsal rib that is holocephalous, or lacking a capitulum.

Caudal vertebrae and haemal arches: Many of the tail vertebrae of *Yandusaurus hongheensis* have been lost, as only five representing the anterior, medial and posterior sections are present, and among them only one is relatively complete, leaving many questions to be resolved.

Anterior caudals: A complete, relatively short and robust centrum is present but lacks its dorsal section. It is 36 mm in length and amphiplatyan with circular anterior and posterior ends. Ventrally, there is a distinct keel, and anteroventrally there are crenulated striations. Posteroventrally, there is a nearly isosceles triangle shaped haemal arch facet. On the dorsal right side there lies a broken remnant scar of a diapophysis, indicating that at its base it was 16 mm in breadth. It is assumed that this centrum is an anterior caudal because it is particularly short, robust, and the haemal arch facet lies only at the posterior end (*Y. multidens* begins to display its haemal arches on the posterior end of the first caudal).

Medial caudal vertebrae: Three specimens are present, among which one is so severely damaged that only from the presence of a haemal arch facet may it be determined to be a caudal centrum. Another caudal displays a broken dorsal neural arch but the rest is well preserved. The centrum is amphiplatyan and generally circular. The ventral surface is round and smooth and lacks a laminar keel. Laterally it is also smooth and lacks crenulated striations. Haemal arch facets lie both antero- and posteroventrally with the anterior small and resembling an inverted triangle. The posterior facet is much larger and appears as a rounded arc. Diapophyses extend laterally and horizontally from the dorsal centrum. The centrum is 40 mm in length and 31-32 mm in diameter.

The third caudal (see Fig. 28-A) lacks its right side but the rest is relatively well preserved. Its morphology resembles that described previously but its diameter is smaller, the anterior haemal facet is smaller than the posterior facet, and the diapophysis is also horizontally extended. The neural spine is posteriorly inclined at an approximate 50° angle. A postzygopophysis appears slightly posterodorsal to the midpoint of the neural spine. The centrum is 41 mm in length, anterior diameter is 30 mm, and base of the diapophysis is 19 mm in breadth. These vertebrae are inferred to lie between Cd 10-15 based upon their size, presence of diapophyses, and comparisons made on related taxa.

Posterior caudal vertebrae: Only a single element is preserved. It is 41 mm in length, 23 mm in anterior diameter, and distinctly constricted at its mid point. It is amphiplatyan and lacks diapophyses. Ventral preservation is too poor to determine the presence of haemal arches.

Haemal arches: Only a single element is preserved that is extremely small, 35 mm in length, and 14 mm anteroposteriorly. It is "Y" shaped and clearly represents a medial to posterior element.

Pectoral girdle and anterior limb: Preserved are a left and right scapula, left coracoid and incomplete right coracoid. A sternum is not recognized and a clavicle is probably not developed. The anterior limb preserves a left and right humerus, radius, a portion of metacarpals, phalanges, and unguals. The ulnae and carpals are missing.

Scapula: Both left and right elements have suffered some damage, but supplementary reconstruction allows the description of morphology and size (see Pl. IV-1, 2). The medial section is distinctly thickened, laterally it is swollen, and the dorsal (distal) end is relatively thin but appropriately broadened. Morphologically, there is no noticeable distinction between these scapulae and those on *Y. multidens,* with the predominant differences lying in the size and ratio to humerus length. Measurements are as follows:

Left scapula-coracoid length	289 mm
Left scapula length	260 mm
Right scapula length	264 mm
Right scapula breadth of distal end	93 mm
Left scapula smallest breadth of shaft	51 mm
Left scapula greatest thickness of shaft	22 mm
Right scapula general thickness at distal end	~5 mm

Coracoid: A left coracoid is completely preserved (see Fig. 28-B, Pl. V1-1) that is laterally convex, medially concave, and is longer anteroposteriorly than dorsoventrally. In outline it is slightly pentagonal. The coracoid foramen is elliptically shaped and situated midway dorsolaterally while penetrating the coracoid at an oblique angle to the medial side. It reaches the midpoint of the dorsal margin to unite with the proximomedial margin of the scapula and composes a lenticular shaped depression. The posterolateral glenoid fossa is semicircular with its largest dorsoventral diameter being 45 mm. On the anteroventrolateral side there is a distinct keel that attenuates near the center of the coracoid. A crescentic depression lies posteriorly and extremely

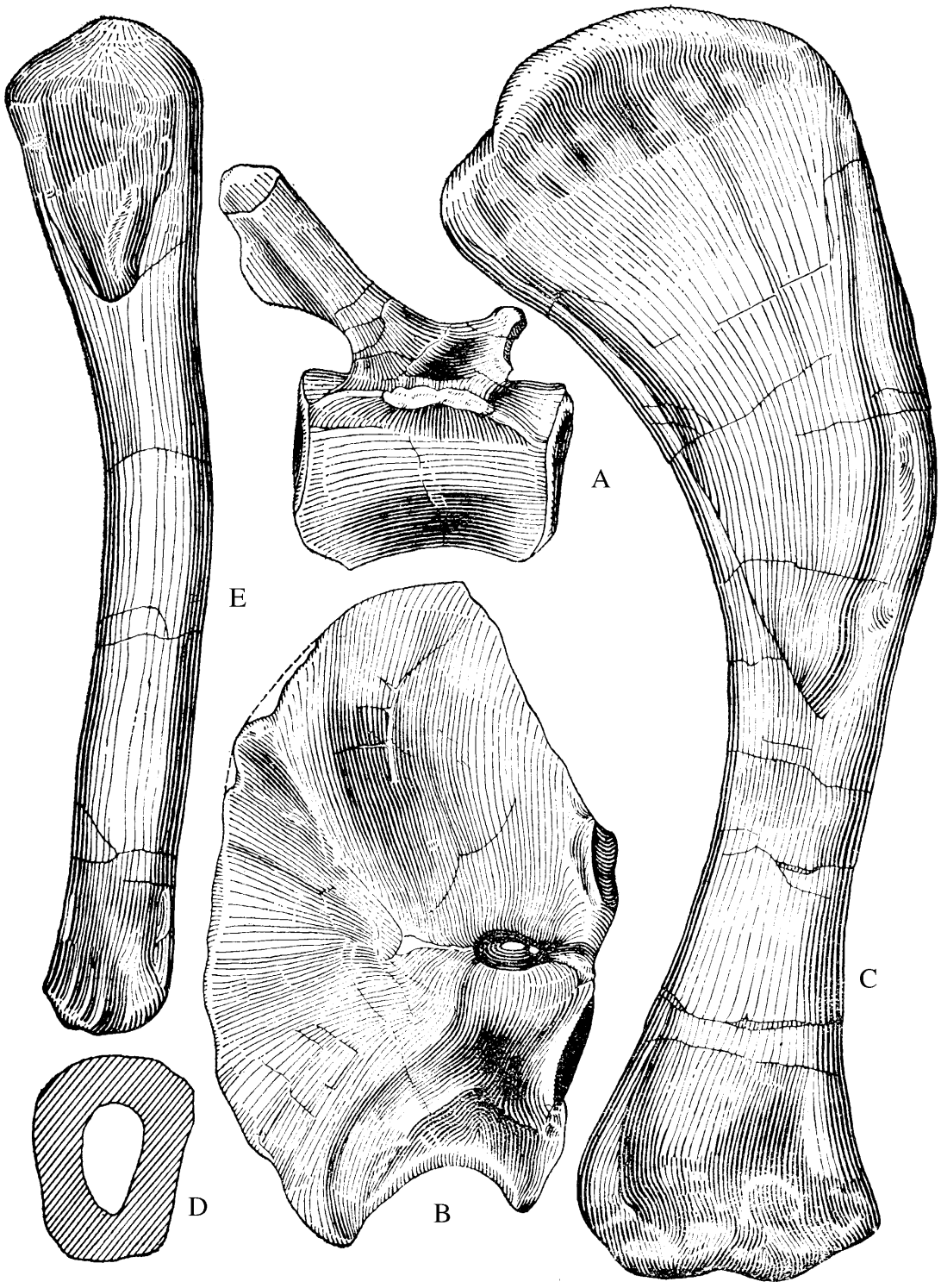

Figure 28. *Yandusaurus hongheensis*
A. Right view of medial caudal vertebra (x 1); B. Lateral view of left scapula (x 1); C. Anterior view of left humerus (x 2/3); D. Cross-section of right humerus shaft (x 1); E. Radius (x 1).

close to the ventral side of the glenoid. The greatest thickness of the coracoid lies within the glenoid fossa where it reaches 25 mm. Its thinnest point is at the distal margin where it is merely 3-4 mm. Its greatest anteroposterior length is 105 mm and dorsoventral length is 63 mm. The preserved morphology of the scapula-coracoid suggests the absence of a clavicle.

Humerus: The humerus is nearly as long as the scapula with a distinctly rotated shaft and well-developed deltopectoral crest located proximally and terminating near the midline of the shaft (see Fig. 28-C, Pl. VI-3). Both proximal and distal ends are equally broad with the narrowest point of the limb at the center of the shaft. Medial curvature is extremely conspicuous and forms a regular arc. The proximal end is also dorsally projected to form an arc, its center is thickened, but toward both sides it narrows distinctly. At the distal end the medial condyle is projected anteriorly while the lateral condyle correspondingly projects posteriorly. The trochlea is very weakly developed posteriorly but anteriorly is slightly deeper and extends dorsally for a short distance before attenuating. The shaft is hollow with extremely thick walls and is infilled with calcite (see Fig. 28-D). Measurements are as follows:

	Left	Right
Length	260 mm	259 mm
Proximal breadth	83 mm	80 mm
Distal breadth	63 mm	68 mm
Smallest shaft diameter	31 mm	30 mm

Radius: The proximal articular surface is subtriangular or a nearly perfectly rounded triangle (see Fig. 28-E) that is 29 mm in breadth. In cross-section at its midpoint the shaft is nearly circular and completely rotated. Its length is 153 mm, or roughly 59 percent the length of the humerus. This may represent the the smallest humeral-tibial ratio among the hypsilophodontids (on *Y. multidens* this ratio is 68.3%)

Forelimb: Carpals are absent, but two metacarpals that may represent Mc II and Mc III from both the left and right sides are present. Those on the left side are complete with lengths of 52 mm and 53 mm (see Pl. IV-6, 7), but only the proximal portions of the right side are present. The proximal ends are distinctly inflated and rather semicircular in cross-section. The ventrolateral sides are concave and the center of the shaft is constricted. The distal ends are also inflated with depressions medially and laterally and a very slightly developed intercondylar groove. There are only several phalanges with a distinct medial keel on their proximal articular surfaces (see Pl. VI-8). Two ungual phalanges are 34 mm and 25 mm long, clawed, dorsoventrally flattened, and are anteriorly sharp and gracile (see Fig. 29-C, Pl. V-4, 5).

Hindlimb: The pelvic girdle of *Y. hongheensis* is completely lost, with the exception of a small fragment. The hindlimb is also extremely incomplete with only a proximal femur and right distal femur, proximal left tibia, and distal left and right fibulae, in addition to incomplete metatarsals, phalanges, and several unguals.

Femur: Only 89 mm of a proximal femur is present with a damaged head, a partially damaged lesser trochanter that is triangular in cross-section and separated from the greater trochanter by a deep cleft, and an indistinct but constricted neck. The proximal end of the shaft is nearly a perfectly rounded triangle in cross-section. The femoral wall attains 10-13 mm in thickness. A 126 mm section of distal femur is preserved that is 77 mm broad. The medial condyle is distinctly larger and positioned more dorsal than the lateral condyle (see Fig. 29-A). Posteriorly, the intercondylar groove is 13 mm broad and 24 mm deep. Anterodistally a trochlea is absent. In cross-section the distal shaft is nearly circular. The fourth trochanter is not preserved.

Tibia: The articular surface of the left proximal tibia is relatively flat and smooth and slightly laterally inclined. The cnemial crest has been broken. The mediolateral breadth is 68 mm,

the medial and lateral condyles are nearly equivalent in size (see Fig. 29-B), and the proximal shaft is nearly triangular in cross-section.

Fibula: Less than 45 mm of the left and right distal fibulae are preserved. The distal shaft is relatively flat and 24 mm wide. The articular surface is distinctly inflated and shaped like a perfectly rounded triangle.

Pes: A single distal metatarsal is represented in addition to several distal pieces of phalanges and a single incomplete ungual phalanx. The distal metatarsal is circular in cross-section with a diameter of 18 mm. The articular surface is projected but slightly concave laterally. The distal phalanges are 22-28 mm and on each lies a dorsal triangularly shaped fossa. Morphology of the unguals on the pes is similar to that on the manus, only the dorsoventral curvature is slightly less and it is a larger element, being 42 mm in length.

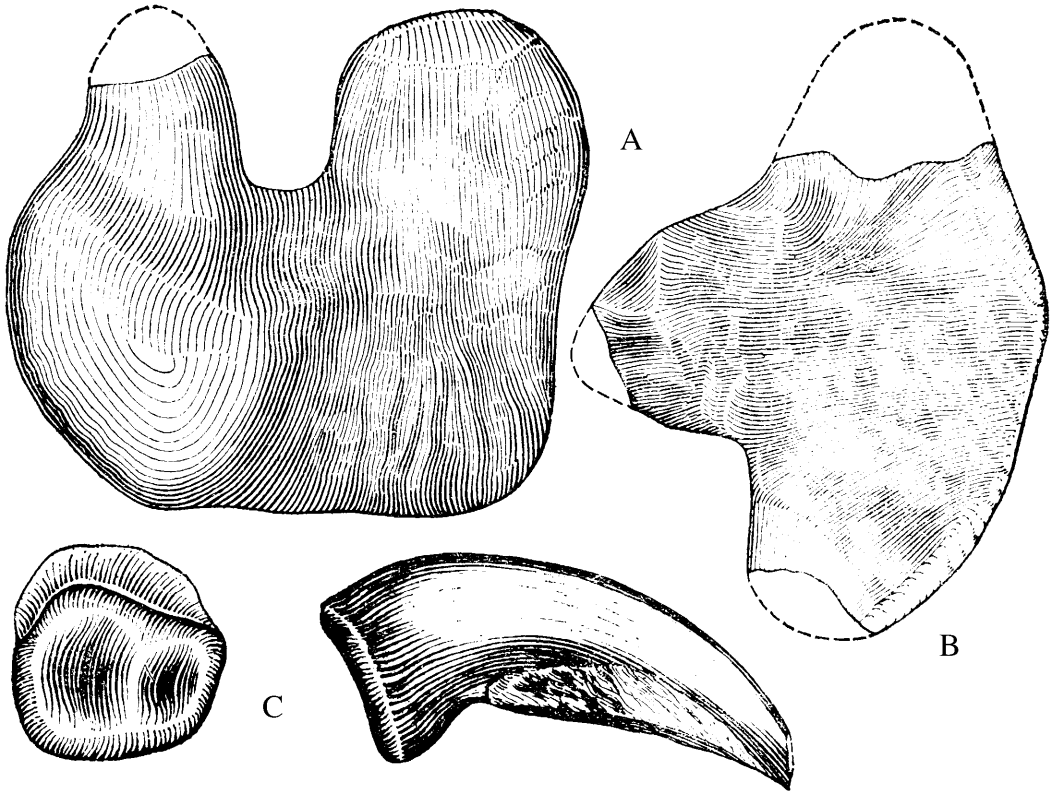

Figure 29. *Yandusaurus hongheensis*
A. Distal view of left femur (x 1) ; B. Proximal view of left femur (x 1); C. Lateral and posterior view of anterior ungual phalanx (x 2).

Ossified tendons: Due to the lack of complete vertebral specimens, there is no evidence for the presence of associated ossified tendons, although in the course of preparation, several long slender tubular features were recognized in the matrix that were uniform in thickness, elliptical in cross-section, and approximately 1-3 mm at their largest diameter. These can be nothing else but ossified tendons.

Size of *Yandusaurus hongheensis*: An accurate assessment of length and size is not possible due to the incomplete nature of the specimen, and particularly due to the poor quality of the caudal vertebrae and hindlimbs. However, some basic estimates may be conducted: the size of the mandible compared to those on skulls of related taxa suggest that the skull should have

exceeded 200 mm. The preserved length of the five cerviclal vertebrae is 237 mm. If it is assumed that there are nine vertebrae in the sequence, then the total length should be 400 mm or slightly longer, assuming that there was not a large variation in length along the column. This species should not have exceeded 3 m in total length. The forelimb (humerus, radius, and Mc III) is 466 mm. Because this taxon is bipedal and adapted to rapid cursoriality, the length of the posterior limb bones should have greatly exceeded the length of the forelimbs. On *Y. multidens* the forelimb is 44-47 percent of the hindlimb, while on *Hypsilophodon foxii* this ratio is 52.2 percent. Consequently, it is estimated that the hindlimb of *Y. hongheensis* (femur, tibia, Mt III) should be approximately 900 mm or slightly longer.

The 3 m length of *Y. hongheensis* exceeds that of other primitive ornithischians, as *Lesothosaurus diagnosticus* is approximately 1 m, the largest measurement for *Hypsilophodon foxii* is 2.27 m, the reconstructed skeleton of *Dysalotosaurus lettow-vorbecki* is 2.6 m, and *Laosaurus consors* is 3.25 m. All individuals of *Y. multidens* are smaller then *Y. hongheensis*; consequently, the latter is recognized as the largest in the genus.

Comparison of *Y. hongheensis* and *Y. multidens*

Yandusaurus hongheensis was collected from the Upper Shaximiao Fm. at Hongheba Dam, east of Zigong, while *Y. multidens* was recovered less than 10 kilometers away from the Lower Shaximiao at Dashanpu, northeast of Zigong. A conchostracan marker bed lies at the center of the Shaximiao Fm., allowing the recognition of the upper and lower members of the formation, both of which constitute terrestrial fluvio-lacustrine red beds. As these two species of hypsilophodont dinosaurs were recovered from geographically and geochronologically close localities, they share more morphological similarities than dissimilarities; or more importantly, their shared characteristics are primary, while their distinctions are secondary.

Table 15. Distinctions between *Y. hongheensis* and *Y. multidens*.

	Y. hongheensis	*Y. multidens*
Size	Larger	Smaller
Quadratojugal	Short and broad	Narrow and long
Lateral temporal fenestra	Ventrally narrow	Ventrally broad
Maxilla	Tooth count fewer (15)	Tooth count more (18)
	More dental denticles (5-6 per side)	Fewer dental denticles (average of 3 per side)
	Relatively thin vertical ridges	Relatively thick vertical ridges
Scapula length	Equivalent to humerus length	Shorter than humerus
Coracoid	Clear anterolateroventral ridge	No anterolateroventral ridge
Humerus	Proximally broad with large posterior curvature	Proximally narrow with slight posterior curvature
Hind claws	Broad	Narrow

The two species share extremely similar maxillae with a lateral inflation dorsal to the tooth row with four to five small foramina upon it, and a dorsal laminae or process that is small and distinctly posteriorly inclined. The morphologies of jugals and maxillae are similar, forming a large orbit and triangular antorbital fenestra. The maxillary dentitions display both anterior and posterior basal margins of tooth crowns with distinct lateral ridges. All teeth lack median keels, which is characteristically different from other taxa within the Hypsilophodontidae. Both taxa share morphologically similar vertebrae, although the sacrum of *Y. hongheensis* is still not known. Vertebrae have the form of distinctly medially constricted amphiplatyan cervicals with

well-developed ventral keels posterior to Cv4 and neural spines that are small and triangular in outline. Dorsal centra are extremely similar in outline, and have neural spines that are nearly perpendicular plate-shaped rectangles. Parapophyses are lost on (at least one of) the most posterior dorsals where the ribs are holocephalous. Caudals are also extremely similar. Scapulae are distinctly anteriorly expanded and relatively broad and short. Further comparisons of posterior limbs and pelvic girdles are not possible due to lack of data. Finally, the unguals are clawed. Characters that justify species differentiation are listed in Table 15.

Section III Discussion of *Yandusaurus*

The Relationship of *Yandusaurus* to Other Ornithischia in the Sichuan region.

The geographic distribution of ornithischian dinosaurs collected in Sichuan Province to date extends from Anxian Co. west of the Chengdu plain southeastward to Qianjiang Co., and spans the early Jurassic to Late Cretaceous. Taxonomic groups include the Fabrosauridae?, Hypsilophodontidae, Iguanodontidae and Hadrosauridae. With the exception of *Yandusaurus*, the remaining ornithischians are all incomplete or fragmentary to the degree that their taxonomic assignment is questionable. Following is a taxonomic list with associated locality and age data:

Family	Genus & Species	Stratigraphy	Locality
Fabrosauridae?	*Xiaosaurus dashanpensis*	Middle Jurassic, Lower Shaximiao	Dashanpu, Zigong
Hypsilophodontidae	*Yandusaurus multidens*	Middle Jurassic, Lower Shaximiao	Dashanpu, Zigong
	Y. hongheensis	Upper Jurassic, Upper Shaximiao	Hongheba, Zigong
	Y. sp.	Middle Jurassic, Lower Shaximiao	Laoshangou, Kaijiang
Hypsilophodontidae?	Gen. and sp. indet.	Lower Jurassic	Jiangtai, Anxian
Iguanodontidae?	*Sanpasaurus yaoi*	Lower? Jurassic	Buziwan, Weiyuan
Hadrosauridae	Gen. and sp. indet.	Upper Cretaceous	Zhengyan Commune, Qianjiang

***Xiaosaurus dashanpensis* (Dong and Tang, 1983):** This taxon was recovered from the same locality as *Yandusaurus*, and consists of a relatively complete hindlimb, a portion of a front limb, isolated teeth and vertebrae. Dong and Tang recognized the morphology and proportions of the specimen to be fundamentally similar to a hypsilophodontid, which is hereby recognized as valid. Dong and Tang describe the fourth trochanter as a fan-like blade, while that on *Yandusaurus* is strongly pendent (see Fig. 18-C). More importantly, the humerus of *Xiaosaurus* is straight and longer with a humerus/femur ratio approaching four-fifths (79.1%), while *Y. multidens* possesses a curved humerus and *Y. hongheensis* displays a strongly curved humerus. Moreover, *Y. multidens* has very short forelimbs, or less than one-half the the length of the hindlimb with a humerus/femur ratio under two-thirds (65.6-69.8%). The dentition of both genera lack a median keel but both species of *Yandusaurus* display extremely well developed lateral ridges on their upper and lower dentition, which is the most notable character for the genus. It appears that the figured specimen of *Xiaosaurus* lacks any lateral ridges. *Xiaosaurus* was estimated to be 1 m in length, which is an appropriate estimate considering the length of the hindlimb. But compared to *Y. multidens* it should be reconstructed as being a bit smaller. It is uncertain whether *Xiaosaurus* is a juvenile due to the fragmentary nature of the material. Finally, it is significant to note that within the past several years, the excavations at Dashanpu have frequently produced taxonomically diverse assemblages within small areas, and consequently the diagnosis of

disarticulated and isolated skeletal elements may be inaccurate, particularly when the taxa share similar morphological characters.

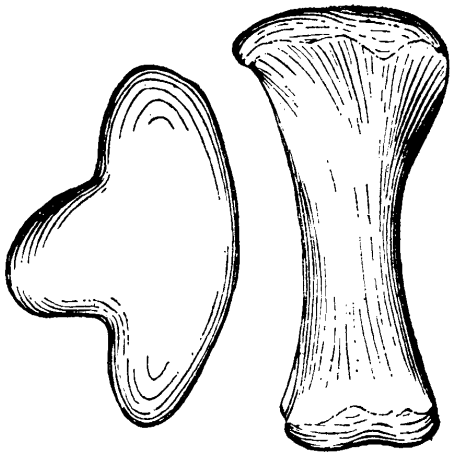

Figure 30. *Yandusaurus* sp. Left, proximal view of tibia. Right, dorsal view of metacarpal (x 1).

***Yandusaurus* sp.:** The specimen was collected from Laoshangou, Jinji Commune, Kaijiang Co. in northeast Sichaun Province from strata thought to be equivalent to the sediments that produce *Y. multidens* at Dashanpu, Zigong, or the Lower Shaximiao Fm. The specimen was discovered by X.L. He in 1970-71. It is regrettable that the specimen is so fragmentary and consists of only a metacarpal and left proximal tibia, which is 33.8 mm anteroposteriorly and 22.9 mm mediolaterally. It is therefore similar in size to *Y. multidens* specimen T6001 but extremely similar in morphology to *Y. hongheensis* (see Fig. 29-B), in that its proximal articular surface is flat and smooth, slightly laterally inclined, lateral and medial condyles are nearly equivalent in size, and lateral condyle is located at nearly the midpoint of the lateral side. The metacarpal is complete and may be a Mc II or Mc III with a length of 41.2 mm. It clearly belongs to a different individual than the aforementioned tibia due to its excessive size. It is, however, slightly smaller than *Y. hongheensis*. This material is diagnosed as assignable to *Yandusaurus* due to the morphological and size similarities in addition to being derived from contemporaneous sediments. The presence of this specimen at Kaijiang indicates that this taxon greatly exceeded the range of Zigong County.

Hypsilophodontidae? gen. and sp. indet.: Specimens were produced from the Early Jurassic Baitianba Fm. at Jiangtai, Anxian Co., Sichuan. Around 1979, Professor B.Y. Bian of the Chengdu Academy of Geology sent to the authors of this paper a few incomplete specimens which consisted of a single incomplete dorsal and caudal vertebra, in addition to some plesiosaur teeth. The dorsal vertebra lacked its neural spine, pre- and postzygopophyses, and distal ends of the diapophyses. The centrum length is 43 mm, anterior breadth is 28.5 mm, anterior height is 31 mm, breadth of the neural spine at its base is 29.7, and breadth of diapophyses at their base are 25.0 mm. It is amphiplatyan with a smooth and rounded ventral surface, lacks longitudinal striations anteriorly and posteriorly, has a neural spine that is thin and plate shaped, and diapophyses that are extended horizontally. Parapophyses are not noted on the portion that is preserved. It is inferred that this is a medial to posterior dorsal (see Fig. 31). The caudal vertebra is missing diapophyses and everything dorsal to its neural arch. It is amphiplatyan with a ventral trough. The anterior facet for the haemal arch is smaller than the posterior facet. The lateral sides are smooth and glossy with only very weak longitudinal striations. Its length is 29.7 mm, anterior breadth is 23.4 mm, and anterior height is 20.8 mm. The breadth of the diapophyses at their base is 11 mm.

The sizes and morphologies of these vertebrae approach *Yandusaurus hongheensis* in characters that include a thin plate-shaped neural spine, smooth and glossy caudal centrum, and other features. They differ, however, in the lack of distinct longitudinal striations on the lateral sides of the dorsal vertebrae, and the broad and deep trough on the ventral side of the caudal vertebrae. These specimens are undoubtedly ornithischian, but too fragmentary to make further diagnoses. As they were produced from Lower Jurassic sediments they may be attributed to either a hypsilophodontid or more primitive ornithischian, and due to their relatively large size they are provisionally assigned to the Hypsilophodontidae, regardless of the fact that the lowest occurrence of this family in Sichuan and England is the Middle Jurassic (Galton, 1975). Further data is required to verify this.

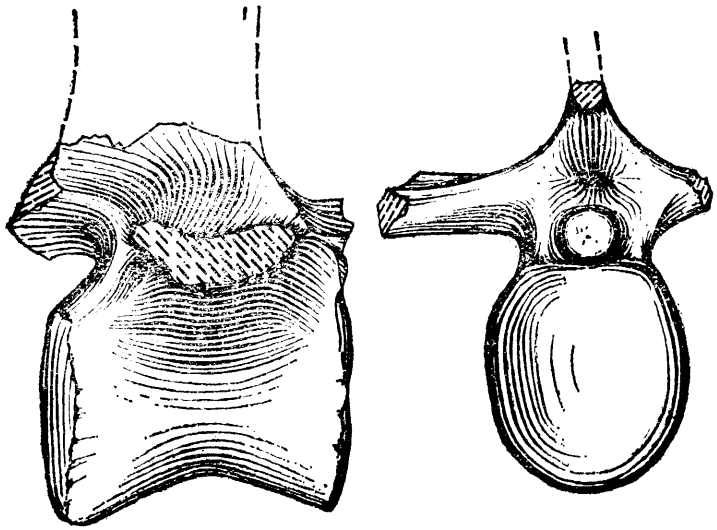

Figure 31. Hypsilophodontidae genus and species indet.
Left, lateral view of dorsal vertebra. Right, posterior view (x 1).

***Sanpasaurus yaoi* Young, 1944:** C.C. Young erected this taxon in 1944 based upon cervical, sacral, and caudal vertebrae, in addition to scapula, humerus, radius, ulna, femur, fibula, phalanges and ungual phalanges. The material is extremely fragmentary, as there are no complete vertebrae or limb bones; however, elements including scapula, radius, and ulna are slightly better preserved. The specimens were produced from Changshanling, Puziwan, in Weiyuan Co. Dong (1983) verified the specimens' stratigraphic position as being the Early or Middle Jurassic Maanshan Member of the Liujing Fm., but the specimens probably represent a composition of taxonomically diverse individuals, and there is insufficient data to assign them to the Iguanodontidae, as characters for taxonomic diagnosis and nomenclature establishment are insufficient. Whether or not the binomial *Sanpasaurus yaoi* should be preserved or a taxonomic revision be undertaken must await the discovery of future specimens from the the same stratigraphic horizon in the Weiyuan vicinity. A previous comparison of *Yandusaurus* to *Sanbasaurus* was made by He (1979), but now with the increase of *Yandusaurus* data, clear distinctions are recognized and further comparisons would be of no significance.

Hadrosauridae, genus and species indet.: Wang (1975) reported the discovery of hadrosaurian teeth and other remains by himself and colleagues in 1974 from Late Cretaceous sediments at Zhenyan Commune (in the Zhengyan Basin), Qianjiang, in southeast Sichuan. This constitutes the only hadrosaur locality in the province. Co-occurring with these specimens were sauropod and carnosaurian dinosaurs. As hadrosaurs are the latest representatives of the Ornithischia and are restricted to the Late Cretaceous, the differences between the hadrosaurine dinosaurs and the hypsilophodontids are extreme both geographically and geochronologically, and there is no reason to discuss this material any further in relation to *Yandusaurus.*

The aforementioned descriptions summarize all the ornithischian data recovered to date from Sichuan Province, but perhaps do not accurately reflect the actual conditions, as specimens are fragmentary, sparse, and damaged. Much more data is required prior to advancing further discussions. However from the perspective of the data at hand, primitive hypsilophodontid dinosaurs are recognized in the Early, Middle, and Late Jurassic of Sichaun Province, which suggests the possibility of recovering much more data. The current finds cannot be regarded as merely fortuitous as the expansive geographic range spans the regions from Kaijiang to Anxian Co. and the expansive chronologic range spans the Early to Late Jurassic.

The Phylogenetic Relationships and Taxonomic Position of *Yandusaurus*

R.A. Thulborn (1977) and P.M. Galton (1974) recognized two grades of Ornithopoda: the Dolichopoda and Brachypoda. The former is primitive with a gracile skeletal structure adapted for cursoriality. They have a small skull, long hindlimbs, a femur that is shorter than the tibia, and Mt III exceeding one-half the length of the femur. This group includes such families as the Fabrosauridae, Heterodontosauridae, Hypsilophodontidae, and Psittacosauridae. The Brachypoda were derived from a lineage of the Dolichopoda and roamed with a more moderate gait. They possessed a large skull, had a femur that was longer than their tibia, and an Mt III shorter than one-half the length of the femur. This grade includes such families as the Iguanodontidae and Hadrosauridae. There is no doubt that *Yandusaurus* may be included within the Dolichopoda.

Although spatial distances are relatively great between the occurrences of the relatively complete and primitive East Asian ornithischians and those from Africa, Europe, and North and South America, the East Asian specimens are extremely similar to the East African *Dysalotosaurus*, the North American *Dryosaurus*, (which Galton [1981] suggested to synonymize with the former), and the European *Hypsilophodon.* The skulls of the Asian form are particularly similar to *Dysalotosaurus* and *Dryosaurus*, which is the reason *Yandusaurus* cannot represent a higher ranking taxon. Furthermore, its more conspicuous discrepancies, such as its lack of heterodonty, excludes the Chinese form from the Heterodontosauridae and the Cretaceous Psittacosauridae. Identification is therefore restricted to the Hypsilophodontidae and Fabrosauridae.

In 1979 the first publication describing *Y. hongheensis* assigned it to the Hypsilophodontidae, although due to its fragmentary nature, the possibility that it could be assigned to the Iguanodontidae could not be rejected. After the more complete *Y. multidens* were discovered at Dashanpu, these suspicions were negated. Its assignment to the Hypsilophodontidae is based upon cranial size, short rostrum, large and circular orbits, well-developed dental enamel, the absence of a canine, and presence of 9 cervical, 15 dorsal, and 5 sacral vertebrae. These features are consistent with the 9 cervical, 15-16 dorsal, and 4-6 sacral vertebral count of the hypsilophodontids. Amphiplatyan cervical and dorsal vertebrae with thin plate-like rectangular neural spines are also consistent characters between the genera. Diagnostic characters for the genus include broad and short scapula, low ilium with sharp anterior lobe and short and broad posterior lobe, gracile and long posterior pubis, expanded distal ischium, obturator process situated proximally, proximal position of the pendent fourth trochanter, posterior digit formula of 2 3 4 5 and 0, clawed ungual phalanges, which are all also characteristic for the family. Furthermore, skeletal indexes such as the tibia/femur ratio and greatly extended metatarsals (see Table 12) are consistent with many genera in the family. One remaining question remains regarding the presence of a premaxilla, which is unknown due to the preservation of the material. Although premaxillae are present among numerous taxa within the family, it is not confirmed that this feature is present on all taxa (see Table 1). Within the four suborders of the Ornithischia, primitive members of the Ornithopoda, Stegosauria, Ankylosauria, and Ceratopsia all possess a premaxilla, consequently the presence of the premaxilla is primitive for the Hypsilophodontidae and its absence would not restrict its assignment from this family.

Hypsilophodontid taxa similar to *Yandusaurus* include the Early Cretaceous European *Hypsilophodon*, the Late Jurassic East African *Dysalotosaurus*, and the Late Jurassic North American *Dryosaurus*. *Hypsilophodon* shares characters with *Yandusaurus* including its cranial outline, short rostrum, circular orbits, and vertebral morphology and formula. Particularly close are the ventral keel upon the fourth to ninth cervical vertebrae, the initiation of ossified tendons on the fourth cervical, and the hindlimb digital formula. *Yandusaurus* however, differs distinctly in the morphology of its temporal fenestrae (including the antorbital fenestra, upper and lower temporal fenestrae, and nasals) and the morphology of numerous cranial elements (including the

maxilla, jugal, quadratojugal, and others). There are also numerous dissimilarities between their pectoral and pelvic girdles. *Hypsilophodon* also possesses a dorsal ossified maxillary lamina which is completely absent on *Yandusaurus*, and the former displays much better development of ossified tendons. There does not appear to be a close relationship between the two, other than being members of the same family.

Although *Dysalotosaurus* and *Dryosaurus* both occurred in the Late Jurassic, they occupied extremely distant geographical ranges. Galton (1981) recognized numerous shared characters, a limited amount of discrepancies, and suggested a close relationship between these two taxa, even to the degree of synonymizing *Dysalotosaurus* with *Dryosaurus*. The skull of *Yandusaurus* is extremely similar to these two taxa, as are the vertebral count, morphology of the vertebrae, pectoral and pelvic girdles, and limb indexes (see Table 12). Furthermore, forelimb length is less than half the hindlimb length and the scapula to humerus ratio is one or less than one. Although several postcranial discrepancies may be enumerated, they are secondary in nature. It is believed here that from the perspective of postcranial comparisons, the justification for an independent genus in China is unwarranted. The principal distinctions are cranial and dental with the maxillary dental count at 15-18, the mandibular dental count of 20, and all dentition lacking a median keel but possessing well-developed lateral ridges. *Dysalotosaurus* has a maxillary dentition of 13, a mandibular dentition of 11-12, and all teeth displaying a median keel and lacking lateral ridges. The morphologies of the antorbital and temporal fenestrae also differ; the maxilla displays a relatively broad and nearly perpendicular ascending process, and the mandible is proportionally deeper than on *Yandusaurus*. The reconstruction of the posterior cranium on *Dryosaurus altas* (Galton, 1977) is very close to the skull of *Dysalotosaurus*, and a number of characters are shared with *Yandusaurus*, including cranial outline, relatively short antorbital region, large and circular orbits, extended frontals, and the well-developed supraorbital. It is possible there is a close relationship between all three taxa regardless of their geographic isolation.

Colbert (1973) and Galton (1977) both suggested geographic contiguity in the Jurassic between North America, Africa, and Asia, providing opportunities for intermigration. It is noteworthy that to date *Yandusaurus* occurs in the Middle Jurassic and extends into the Late Jurassic, and as such predates the appearances of *Dysalotosaurus* and *Dryosaurus*. The Late Triassic or Early Jurassic South African Stormberg Fm. and East Asian Lufeng redbeds all produce more primitive ornithischians such as *Fabrosaurus* from the former and *Tatisaurus* and *Tawasaurus* from the latter, any of which may have been ancestral to the hypsilophodontids. This raises the question of whether in the Triassic and Jurassic this group was monophyletic with a common ancestor or polyphyletic with parallel lineages in Africa and Asia. These implications are worthy of further research.

The primitive ornithischians from the Late Triassic of Lufeng include *Tatisaurus oehleri* Simmons, 1965, *Tawasaurus minor* Young, 1982, and *Dianchungosaurus lufengensis* Young, 1982, all of which distinctly predate *Yandusaurus* but are geographically nearby. *Yandusaurus* should naturally share a relationship with one of these taxa, and it is regrettable that the data representing them are not ideal, and literature pertaining to them is relatively terse, making it difficult to make further comparisons. Young (1982) assigned *Dianchungosaurus* to the Heterodontosauridae, but compared to the type specimen of *Heterodontosaurus*, aside from sharing the presence of a canine (and even here the position on the premaxilla differs), the two taxa have very different dentitions. *Yandusaurus* differs extremely from *Dianchungosaurus*. Published illustrations indicate a smaller dental count of 12-13 teeth, subcircular to oval crowns in cross-section, very weak denticles, and unobservable lateral ridges.

The photographic plates of *Dawasaurus* are indistinct (Young, 1982) such that comparisons with *Yandusaurus* must be conducted through the text description only. The two share several characters such as a relatively short rostrum, large orbits that are nearly circular in outline, an antorbital fenestra that is triangular with a long base, and a ramus with a horizontal ventral margin.

The distinctions are also relatively clear, as *Dawasaurus* is much smaller with a skull of only 35 mm and it has a relatively large lacrimal. Particularly distinctive is its maxilla that Young stated is "flat with a medial depression at its center," displays 7-9 foramina (*Yandusaurus* possesses 4-5 on its lateral side), has a smaller maxillary and mandibular dental count, and smaller denticles. The published illustration suggests the absence of lateral ridges. As the material is insufficient it is unclear whether there was a close relationship to *Yandusaurus.*

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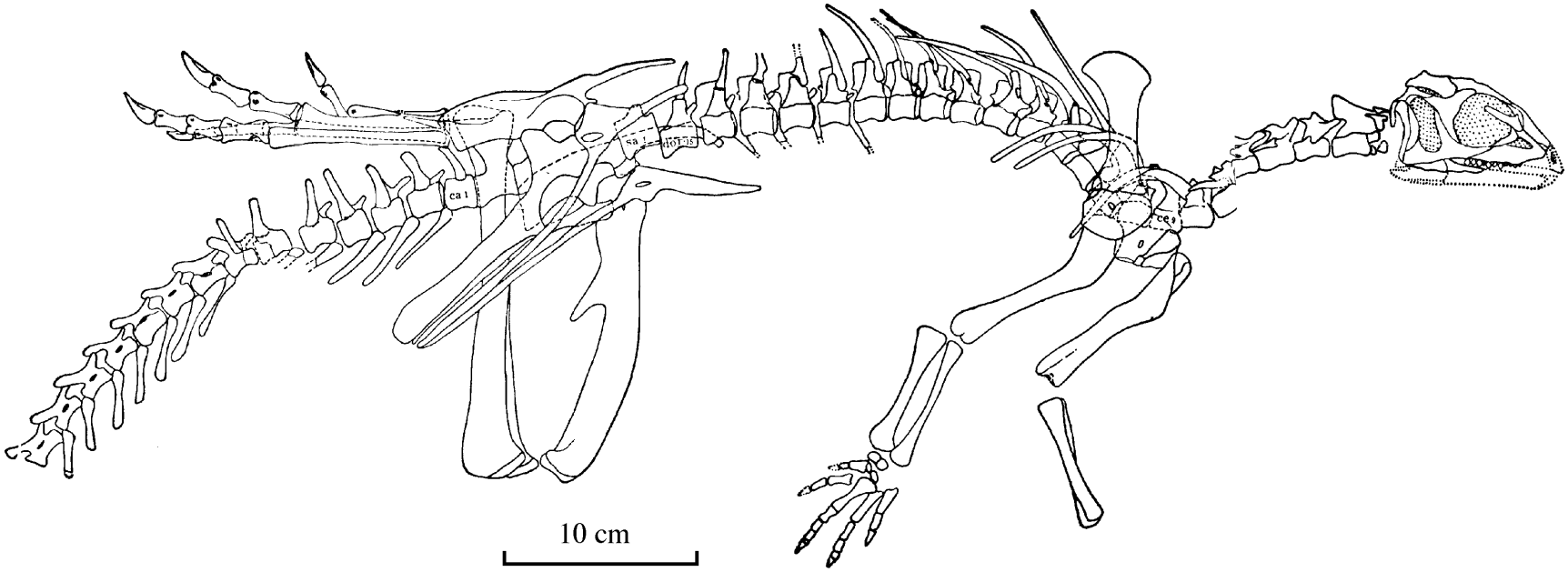

Figure 32. Specimen configuuration of *Yandusaurus multidens* (T6001)

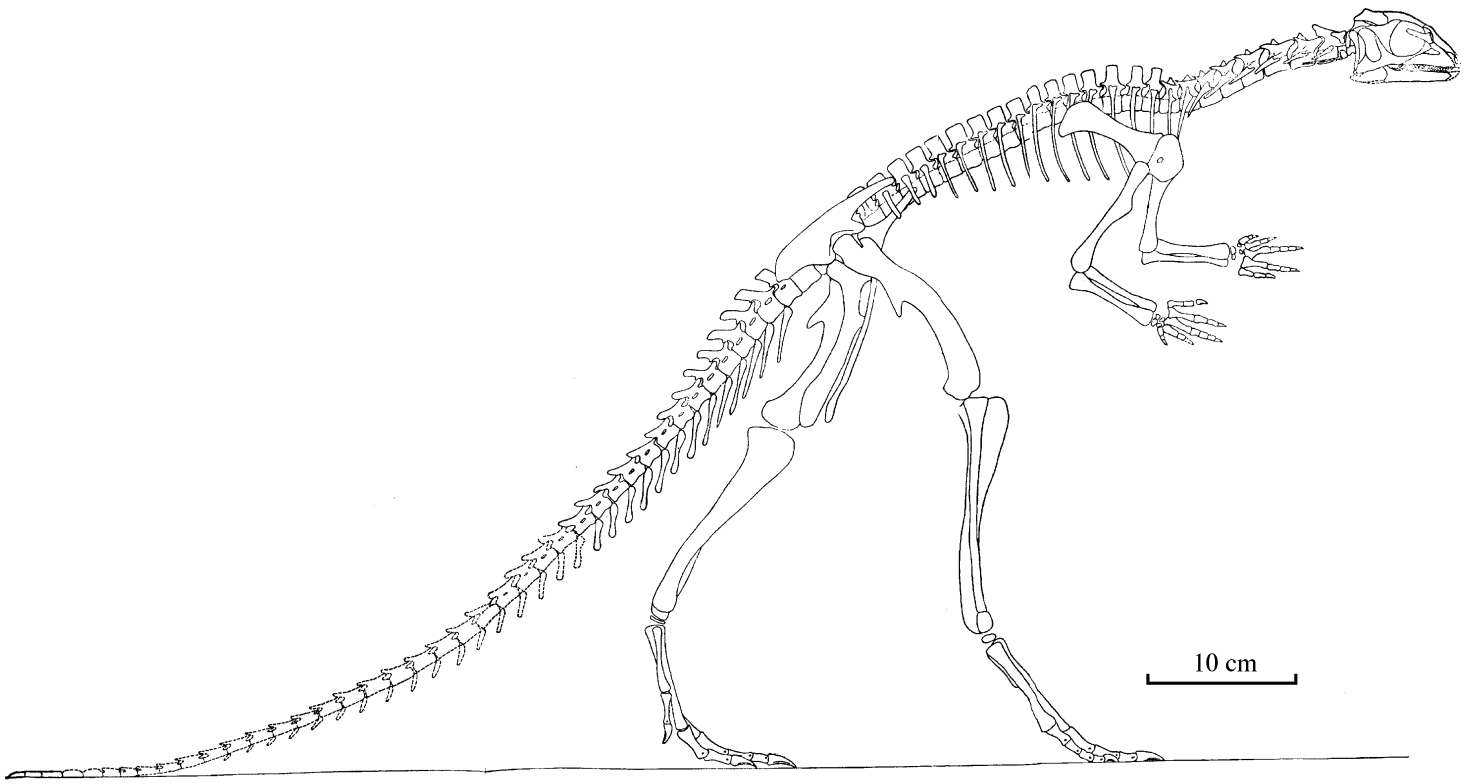

Figure 33. Skeletal restoration of *Yandusaurus multidens* (T6001)