Jurassic Ornithopod *Agilisaurus louderbacki* (Ornithopoda: Fabrosauridae) from Zigong, Sichuan, China

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Abstract

A systematic description of *Agilisaurus louderbacki* from Dashanpu, Zigong, Sichuan is hereby made with a discussion regarding its phylogenetic relationship and taxonomic position. The taxon *Yandusaurus multidens* is hereby reassigned to the genus *Agilisaurus*. *Xiaosaurus dashanpensis* is recognized as an independent genus and species.

Introduction

The Dashanpu fossil quarry at Zigong is a renowned locality. In 1983 Z.M. Dong and Z.L.Tang conducted a study on partial ornithischian skeletons representing two individuals collected from this locality and erected the taxon *Xiaosaurus dashanpensis*. Later, He and Cai (1983, 1984) described two skeletons from this quarry and erected the taxon *Yandusaurus multidens.*

In 1984, when the Zigong Dinosaur Museum was under construction, a nearly complete skeleton was uncovered. A simple description of this specimen was made by Peng (1990) who erected the name *Agilisaurus louderbacki.* Because this specimen is one of the most complete small ornithopods known in the world to date, it is extremely significant to the discussion and analysis of relationships, morphology, and biogeography of small ornithopods.

Description

Ornithischia Seeley, 1888

Ornithopoda Marsh, 1871

Fabrosauridae Galton, 1972

Agilisaurus Peng, 1990

Agilisaurus louderbacki Peng, 1990

(Figs. 1-6; Pls. I-III)

Etymology: *Agilis,* Latin for an agile bipedal animal, as indicated by the light structure of the skeleton and limb ratios. The species epithet is in honor of the late U.S. geologist Dr. George D. Louderback, the first scientist to discover dinosaur fossils in the Sichuan Basin in 1915.

Diagnosis: The skull is short and high, with parietals distinctly constricted at their center, and long nasals that possess a longitudinal depression lying at the center of the suture. The posterior process of the maxilla does not contact the lacrimal. Buccinator fossae on the maxilla and mandible are distinct. The antorbital fenestra is located dorsally and the orbit is situated at the posterior half of the skull. The supraorbital is well developed with a posterior extension that attaches to the lateral side of the postorbital to split the orbit into upper and lower fenestrae. The quadrate is robust and transversely inflated at the condyle. The coronoid process of the mandible is high, the articular fossa is situated low, and a mandibular fenestra is absent.

The dental formula is $\frac{\text{Pmx } 5 + \text{Mx } 14}{\text{D } 20}$ with premaxillary caniniform teeth that shear against three anterior teeth on the dentary. Maxillary and mandibular tooth crown shapes are either triangular or rhomboid.

The axial skeleton is composed of 9 cervical, 15 dorsal, 5 sacral, and 44 caudal vertebrae. Cervical and torso regions are short, while the caudal region is long, constituting over one-half the total length of the body. Ossified tendons are restricted to the dorsal and sacral regions. The scapula is shorter than the humerus. The ilium is long, as is the club-shaped pubis. The obturator process is located at the proximal third of the ischium. The lesser trochanter of the femur is situated lower than the greater trochanter and is separated from the latter by a deep cleft. A small nutrient foramen is located on the femoral shaft lateral to the pendent fourth trochanter. The tibia is longer than the femur and the Mt III is longer than one-half the length of the femur. The digit formula is 2 3 4 5 0. Ungual phalanges are all clawed.

Type: Specimen ZDM 6011 (Zigong Dinosaur Museum catalog number) consists of a nearly complete skeleton that lacks only a portion of its left fore limb and left hind limb.

Locality and stratigraphic position: Middle Jurassic, Lower Shaximiao Fm., Dashanpu, Zigong Co., Sichuan Province.

Description: The skull is short and high. In lateral perspective it appears bluntly triangular, while dorsally it is wedge shaped. The occipital region is broad and slightly anteriorly askew due to compressional distortion. The supraoccipital is rhomboid shaped, slightly higher than broad, and located at the center of the occipital region where it forms the dorsal margin of the foramen magnum. At its center lies a nose-like longitudinal ridge that accommodates cervical ligaments. Exoccipitals lie lateral to the foramen magnum, are thickened medially, and fuse ventrally with the basioccipital to compose the occipital condyle. Laterally there are two small foramina, the anterior representing cranial nerve XI and posterior representing cranial nerve XII. The lateral sides of the exoccipital are thin and extend ventrally to form the angularly shaped paroccipital process. The basioccipital composes a majority of the occipital condyle which is indistinct in morphology due to its breakage within the cervical region. From the basioccipital region anteriorly lies a medial ventral ridge that is fan shaped and slightly concave on both lateral sides. Its anterior margin fuses with the basipterygoid.

The basipterygoid is located anterior to the basioccipital and anteromedially it is longitudinally concave, while laterally both sides are inflated to form rounded and smooth longitudinal ridges. An anterior basipterygoid process is not well developed. The parasphenoid arises from the anterior region of the basipterygoid, but only its posterior flattened club-shaped portion is visable due to obstruction by the left hyoid.

The laterosphenoid is laterally convex and forms the lateral wall of the braincase. Its dorsal margin connects to the frontal and postorbital. The prootic is long and narrow and extends vertically to lie between the laterosphenoid and parietal. Its posterior margin is overlain by the parietal. An opisthotic is not noted.

The pterygoid is thin and plate shaped with an irregular morphology. Posteriorly it is butterfly shaped and has a long posterolaterally inclined projection that contacts the medial lamina of the quadrate. The anterior process is correspondingly small and extends anteriorly to cover the ventral surface of the ectopterygoid. The ectopterygoid is located anterolateral to the pterygoid with a distinct embayment and strong dorsolateral rotation that connects with the jugal. A triangular element, representing the palatine, lies on the right side anterior to the pterygoid and ectopterygoid. This element's relationship to the maxilla is unclear due to compressional distortion.

The parietal is short and fused with a sagittal crest. Anteriorly the suture for contact with the frontal forms a broadened "V" but a median process is absent. A medial constriction of the parietal is more noticeable than on *Yandusaurus multidens* (He and Cai, 1983). This element composes the posterodorsal wall of the braincase. Posteriorly it increases in breadth and rotates

dorsally to form the posterior wall of the supratemporal fenestra and to connect with the squamosal. The frontal is relatively large and broad and constitutes approximately one-third the total length of the skull. The median suture is straight with a lateral margin that is acute, crescentically shaped, and forms the dorsal margin of the orbit. On the dorsal margin of the orbit a distinct muscle scar for the M. ocularis is evident. The prefrontals are yoke shaped, thick at their midpoint, thin around their margins, and overlap the anterolateral frontals and posterolateral nasals. Nasals are triangular with a longitudinally concave and rhomboid-shaped median suture that is deep anteriorly and becomes more shallow posteriorly (Fig. 1-B). Both sides of this depression are gently convex, although the lateral margin is not depressed.

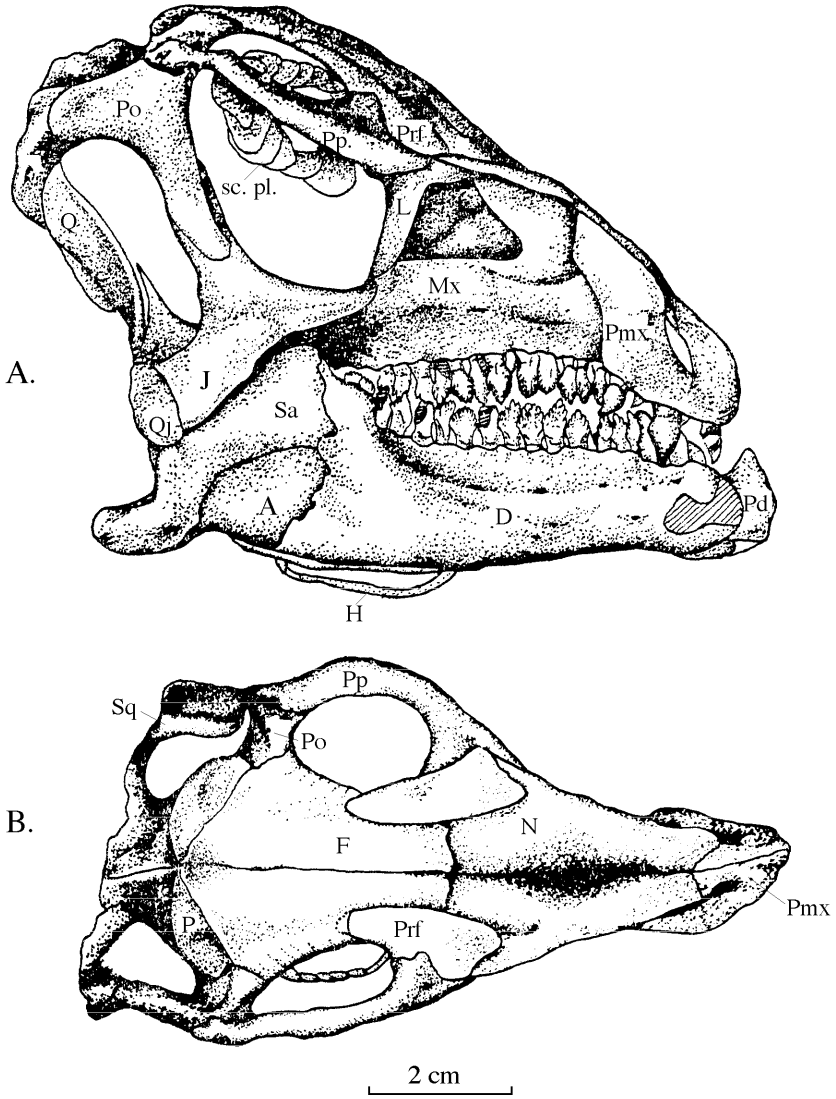

Figure 1. *Agilisaurus louderbacki.* A. Lateral view of skull and mandible; B. Dorsal view of skull.

The rostral portion of the premaxilla is short and sharp with a coarsened surface texture and a median sutural ridge that has a shallow groove at each side. This is very similar to the small angular beak on *Hypsilophodon.* The anterior ascending wedge of the premaxilla penetrates the nasals to divide the left external nares from the right. A posterior process is well developed but does not come in contact with the lachrymal. The maxilla is triangular in shape with a high main body. At its center and running laterally are a series of small nutrient foramina. Ventral to the

foramina series the maxilla is depressed (Fig. 1-A) to facilitate the attachment of the M. buccinatoris. The ascending branch of the maxilla is yoke shaped and separated from the main body by a laterally depressed scar, which may be the vestige for a dorsal blood vessel. A bony lamina projects posteriorly from the anteromedial side of the maxilla and has a posterior margin that fuses with the medially inclined lamina of the lachrymal. Together they seal the antorbital fenestra. Only two small antero- and posteroventral angular apertures remain open within this fenestra. The lachrymal is small, club shaped, and lies between the orbit and antorbital fenestrae, with a small lachrymal foramen visible posterodorsally. Dorsally this element curves anteriorly and constricts to a point at its contact with the nasals and prefrontals.

The postorbital is triradiate with a thick and short ascending process that curves medially and a distal end that broadens to connect with the frontal and parietal. The posterior process is short, laterally compressed, and fuses with the anterior process of the squamosal to form the upper temporal bar. The ventral process is long, inclined, and extended anteroventrally, where it overlaps the ascending process of the jugal to separate the orbit from the lateral temporal fenestra. The jugal is also triradiate with an anterior process that is extended and inclined anterodorsally, gradually constricts, and fuses at its inclined ventral margin with the maxilla. The dorsal process is slightly inclined posteriorly and is overlain dorsally by the ventral process of the postorbital. The posterior process is a laterally compressed thin plate that extends posteroventrally to posteriorly cover the dorsal quadrate. The quadratojugal is tear drop shaped and located between the quadrate and posterior process of the jugal at the posteroventral side of the skull. It differs from *Hypsilophodon* by lacking a foramen. Its posterodorsal margin is overlain by the quadrate but its ventral section overlies the quadrate.

The quadrate is nearly perpendicularly extended. Its dorsal articular head is inserted into a depression composed of the squamosal and exoccipital. Its shaft rotates nearly 90° with its ventral end transversely expanded as the articular head for the mandible. The medial side of the quadrate is an anteromedially projecting plate that fuses with the butterfly-shaped process of the pterygoid to form the posteromedial wall of the lateral temporal fenestra. The squamosals consist of a small pair of dorsal angles on the posterior section of the skull. The anterior process is laterally flattened and extends anteriorly to fuse with the posterior process of the postorbital. The posterior process curves ventrally at an approximate 90° angle with a triangularly shaped end that, with the lateral side of the exoccipital, forms the articular depression for the quadrate.

There are five pair of fenestra on the skull in addition to the single foramen magnum that lies occipitally. The external nares are small, slightly elliptical in shape, and anteriorly placed on the rostrum. The antorbital fenestra is quadrate and situated relatively high, with its ventral margin higher than the ventral margin of the orbit. This character differs from that seen in other related taxa. The orbit is large (Table 1) and located on the posterior portion of the skull. Extending across the dorsal section of the orbit is a supraorbital, which divides the orbit into dorsal and ventral fenestrae. The dorsal orbit is small and elliptical while the ventral orbit is relatively large, quadrate, and laterally situated. The supratemporal fenestra is large, nearly triangular, and situated posterodorsally. The lateral temporal fenestra is located posterolateral to the orbit and is perpendicularly extended with broad dorsal and narrow ventral ends. The foramen magnum is nearly circular and composed of the basioccipital, exoccipitals, and supraoccipital.

Mandible: The entire element displays an S-shaped curvature, with a high coronoid process, low articular fossa, and mandibular foramina absent. The anterior end of the predentary has suffered some damage, but there is a cone-shaped ventral process fused to the ventral side of the symphysis, both sides of which project anteriorly and then form into a dorsal cone. This element may have served as an accessory beak. The dentary is long and thick, being low anteriorly, high posteriorly, and slightly convex laterally, except at the dental trough where it is slightly concave, perhaps for accommodating the buccinator musculature. The medial side of the dentary is flat with the Meckelian groove approaching the ventral margin, initiating at the

symphysis, extending horizontally posteriorly, and covered posteriorly by the splenial. Approaching the margin of the dentition there lies another shallow lateral groove that constitutes the dental trough for replacement dentition. The teeth erupt from this groove and the corresponding small foramina. The splenial is thin and flat, lies on the medial side of the dentary, and then wraps around the ventral margin. The angular is anteriorly high and posteriorly low, triangular in shape, and slightly convex laterally. The S-shaped surangular is laterally convex, medially concave, and forms the medial wall of the adductor fossa. It dorsal margin is thick, and anteriorly there lies the high coronoid process. Its posterior section is extended to form a retroarticular process. A prearticular is attached medially to the articular with its dorsal margin medially convex to form an arch-shaped ridge, or the lower margin of the adductor fossa. The articular is elliptical, dorsomedially concave, and slightly medially inclined to form the articular fossa.

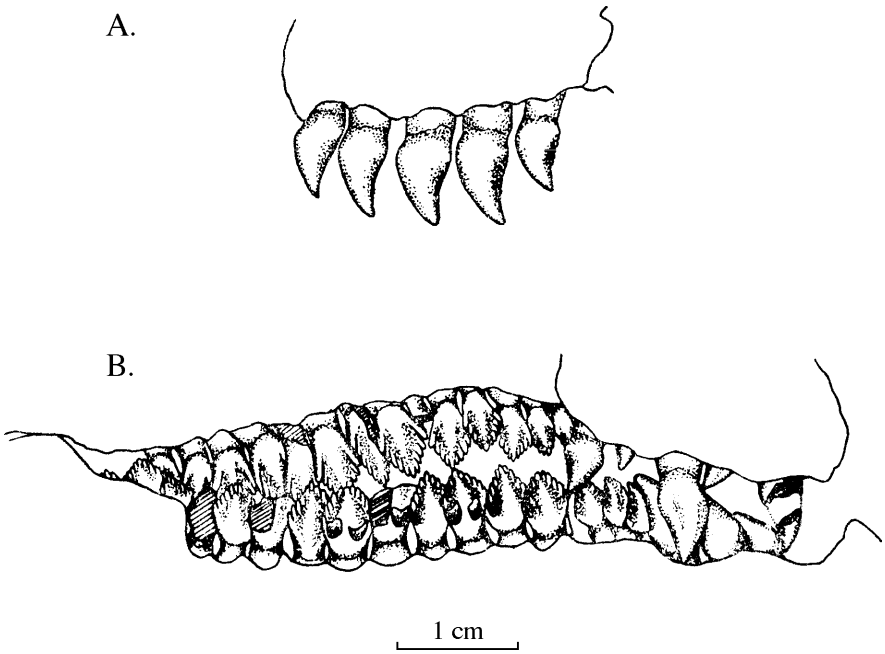

Figure 2. *Agilisaurus louderbacki.* A. Left premaxillary teeth; B. Right dentitions.

Table 1. ***Agilisaurus louderbacki*** **Cranial and Mandibular Measurements**.

Element	mm	Element	mm
Cranial length	111.0	Orbit largest diameter	40.5
Cranial height	65.0	Orbit smallest diameter	25.5
Cranial breadth	52.5	Supratemp. fenestra lateral length	17.1
Occipital breadth	50.8	Supratemp. fenestra transverse breadth	17.2
Frontal length	39.0	Lateral temp. fenestra height	31.6
Nasal length	48.8	Lateral temporal fenestra breadth	10.4
Maxilla height	14.0	Foramen magnum diameter	12.5
Antorbital fenestra ventral length	17.5	Mandible length	98.7+
Antorbital fenestra height	11.2	Height at coronoid process	28.0

Dentition: Dental formula $\frac{\text{Pmx } 5 + \text{Mx } 14}{\text{D } 20}$. Premaxillary crowns are slightly laterally compressed, posteriorly curved, and caniniform (Fig. 2-A). Marginal denticles are not well

developed except on the two most posterior premaxillary teeth. A conspicuous diastema is not present between the premaxilla and maxilla. Cheek teeth are in close alignment and slightly imbricated anteroposteriorly. Crowns are triangular or rhomboid shaped and are noticeably higher than broad as on *Fabrosaurus*. Enamel is equally thin on both lingual and labial sides of the teeth. Crown apices are frequently composed of three denticles. As a result, the anterior and posterior margins of the teeth consist of 4-5 basically symmetrical anterior and posterior denticles. Chisel-shaped wear facets are noted only on various posterior teeth. Cingula are absent. Maxillary teeth do not possess distinct lateral keels. Three anterior mandibular teeth are morphologically similar to the anterior maxillary teeth and these sets shear against each other. The remaining posterior mandibular teeth are similar to the maxillary teeth, although at the lateral base of the crown there is a small and deep semicircular or crescentic pit which may be the result of wear by the maxillary teeth. Replacement teeth erupt from the top of the lingual wall of the maxillary and mandibular dental trough. Their morphology is basically similar to the functional dentition, but with more gracile denticles.

Accessory elements: A supraoccipital is club shaped with a distinctly expanded base that forms a sinuous curve with the frontal suture. The shaft gradually constricts posteriorly and becomes laterally arched. The posterior end is laterally flat, becomes rhomboid shaped, and is tightly fused to the post orbital. This, in effect, splits the orbit into a dorsal and ventral fenestra.

An elliptically shaped sclerotic ring is preserved in the right orbit that is composed of numerous thin plates, the precise number of which is indeterminate due to their overlapping by the prefrontal and frontal. It is estimated that their count is probably equivalent to those of *Hypsilophodon,* or 15. Each plate is elliptical or rhomboid shaped, slightly concave laterally, and arranged as imbricated tiles. The entire ring is laterally convex, 26.5 mm in largest exterior diameter, and 18 mm in smallest diameter.

Medial to the mandible is a 45 mm long bone, thin and club shaped, with clear lateral striations on its surface. The anterior end is slightly inflated, central section is curved, and posterior section slightly flattened. This is recognized as the first ceratobranchial of the ossified hyoid apparatus.

Axial Skeleton

Vertebrae and ribs: Specimen ZDM6011 preserves 73 articulated vertebrae. The presacral region is relatively short while the caudal region is long, constituting over one-half the length of the body.

Nine cervical vertebrae are present for a total length of 17 cm. A left and right proatlas are each triangular, laterally compressed, and anteroposteriorly extended. An atlas intercentrum is 8 mm long, 14.5 mm wide, and subcrescentically shaped in dorsal perspective. Dorsally there is a shallow and broad concavity for articulation with the occipital condyle. The left and right neural arches are triradiate, unfused, and encircle the dorsolateral section of the occipital condyle. The atlas rib is holocephalous and extends to the midpoint of Cv3. The axis is platycoelus with a small odontoid process anteriorly. A neural spine is high and expands posterolaterally to form an anteroventrally inclined plate. The axis rib is spear shaped with a small projected capitulum to make it dichocephalous. Cv3-9 are opisthocoelus with small triangular neural spines. The ribs are gradually broadened proximally, the shafts increase in length, and the curvature increases posteriorly.

There are 15 dorsal vertebrae for a total length of 29 cm. Centra are amphiplatyan and rectangular, and lack ventral keels and lateral depressions. Diapophyses are horizontally extended. Anterior dorsal ribs are relatively long with relatively large curvature, while the posterior ribs gradually shorten and straighten. The most posterior dorsal ribs are holocephalous.

There are five sacral vertebrae present in various degrees of fusion. Both ends of the centra are distinctly swollen with breadth larger than height. Lateral depressions and ventral keels are absent. Neural spines are relatively low, broad, and thick. Diapophyses are inflated at their base to become fused with the lateral sides of the prezygopophyses, and have distal ends that are fused with the sacral ribs. Two anterior sacral ribs are relatively thin, inclined anteroventrally, and distally do not contact the ilia. This indicates that the two anterior sacrals were initially dorsal vertebrae and are now in a transitional state. Three posterior sacral ribs are horizontally extended, swollen at their distal ends, and contact the illia.

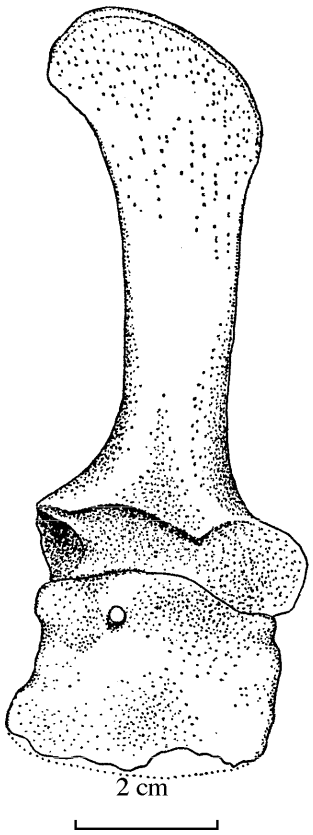

Figure 3. Lateral view of *Agilisaurus louderbacki* right scapula.

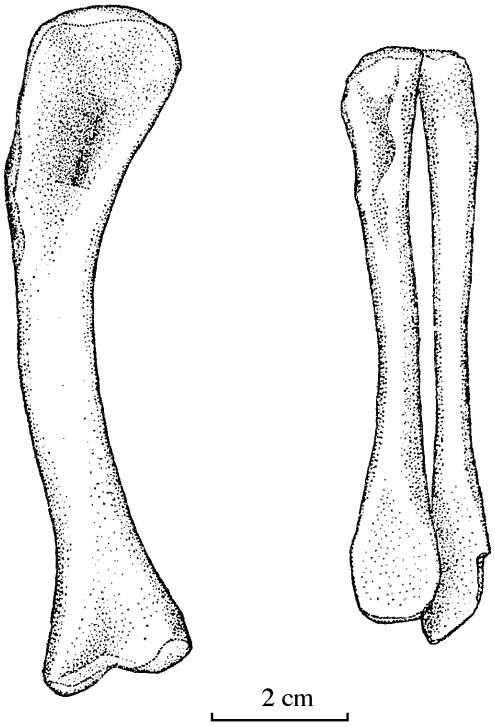

Figure 4. Anterior view of *Agilisaurus louderbacki* right forelimb. A. Humerus; B. Radius and ulna.

There are 44 caudal vertebrae present with a total length of 107 cm. Centra are amphicoelus. The longest in the column is Cd 20 which is 26.7 mm. On the anterior four centra ventral keels are rather distinct, but these become lost on the mid-caudals, and on the posterior caudals a longitudinal ventral depression is present while there are rounded and smooth longitudinal ridges laterally. The most posterior caudals are small, laterally compressed, and probably represent the termination of the tail. Neural spines gradually lower anterior to posterior, with a gradual decrease in angle to the centrum, such that at the posterior end they become essentially parallel. Diapophyses of anterior caudals are long but gradually shorten with their base increasing in breadth posteriorly. At the middle caudals the diapophyses become the aforementioned longitudinal ridges on the lateral sides of the centra, and then become lost on the posterior caudals.

Cd1 possesses the longest haemal arch with a laterally flattened and slightly posteriorly curved shaft. Posteriorly the arches gradually diminish in size, the shafts become straight, and the distal ends become broadened and thinned to resemble axe heads, but which are not anteroposteriorly bifurcated. These arches become lost on the posterior caudals.

Ossified tendons: Anteriorly, these features originate at the posterior end of the first dorsal neural spine while posteriorly they terminate at the anterior end of the first caudal neural spine. Ossified tendons are absent on the caudal portion of the skeleton, which differs from both *Fabrosaurus* and *Hypsilophodon*. These features are slender stick-like objects lying in an intersecting arrangement on both sides of the dorsal and sacral neural spines. The lateral side of each spine possesses 3-5 tendons. The longest may exceed seven vertebrae. Individual tendons bifurcate posteriorly with their apices directed anteriorly.

Appendicular Skeleton

The pectoral girdle is preserved relatively completely with a short and broad scapula that is only 84 percent the length of the humerus, and which approaches the length for *Yandusaurus multidens*. The shaft is curved and slightly rotated. It is laterally flattened with a straight anterior margin and crescentic posterior margin. A longitudinal depression lies on the medial side. The distal side is slightly expanded and the distal end is crescentic shaped to facilitate attachment for suprascapular cartilage. The proximal end is distinctly expanded and slightly concave laterally. At the junction of the shaft there is an oscillating ridge (Fig. 3). The glenoid is semicircular. The coracoid is nearly square, relatively thick proximally, thinned distally, and displays a sinuous suture for attachment to the scapula. The coracoid foramen is small and elliptical with a 4 mm largest diameter. Its lateral side is 6.5 mm from the scapula and medial side 2.2 mm. The glenoid is small.

Table 2. Measurements of Pectoral and Pelvic Girdles on *Agilisaurus louderbacki* (mm).

Element	Measurement	Left	Right
Scapula	Length	—	82.0
	Proximal width	—	38.3
	Distal width	32.5	29.0
	Smallest diameter of shaft	16.5	15.0
Coracoid	Length	—	33.3
	Width	—	33.0
Ilium	Length	149.0+	162.0
	Height	32.3	34.7
	Length of anterior lobe	50.0+	68.0
	Breadth of acetabulum	34.5	—
Pubis	Length	220.0+	—
	Length of preprocess	58.5+	—
	Length of postprocess	150.0	—
Ischium	Length	153.5+	164.0
	Proximal width	38.4	—
	Distal width	15.0	14.8
	Smallest breadth of shaft	11.0	11.5

The humerus is gracile, small, and approximately one-half the length of the femur. The proximal end is slightly transversely broadened with a laterally situated humeral head. There is a relatively distinct anterodorsal fossa for muscular attachment. A deltopectoral crest is well developed and located dorsal to the midline of the shaft (Fig. 4-A). The shaft is hollow and

distinctly torsioned. The distal end is transversely broadened with a shallow and broad trochlea. Both condyles are equivalent in size with dumbbell-shaped distal ends.

The ulna is small and gracile with a slightly inflated proximal end and distinct anterior ridge and depression, although an olecranon is not well developed (Fig. 4-B). The shaft is straight and the distal end is broad and flat. The radius is gracile, small, and slightly longer than the ulna. Its shaft is straight, the distal end broad and flat, and its terminal end is pointed.

The morphology and formula of the fore foot is obscured by the vertebral column.

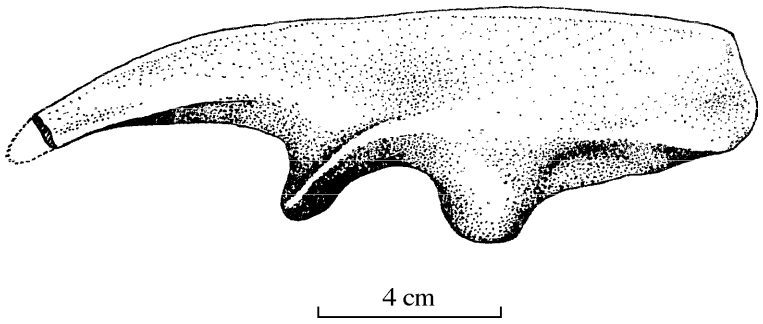

Figure 5. Lateral view of *Agilisaurus louderbacki* left ilium.

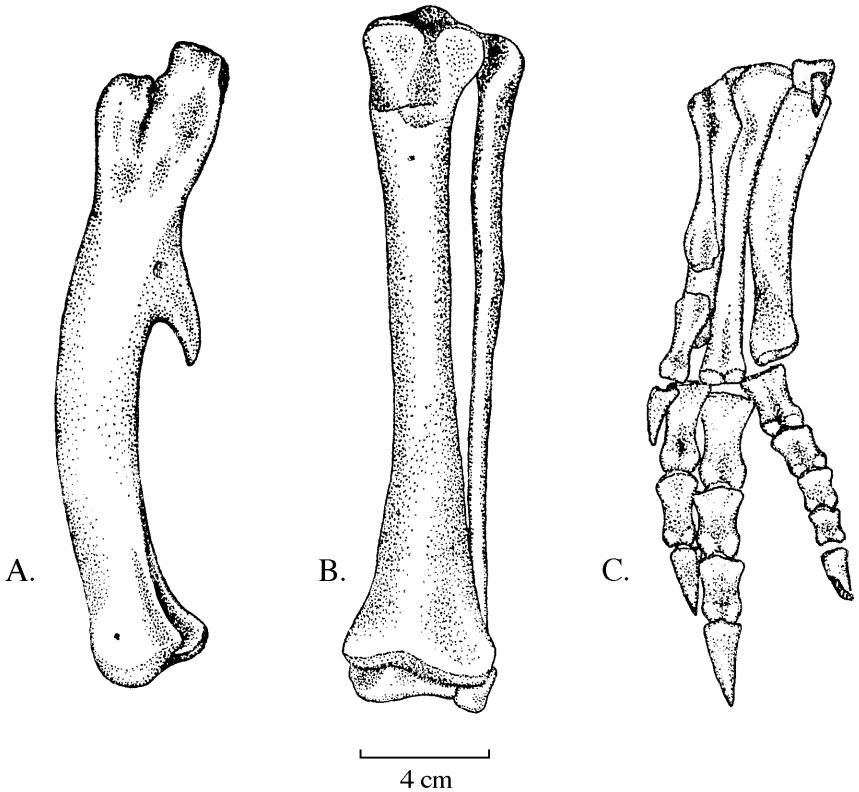

Figure 6. Hind limb and pes of *Agilisaurus louderbacki.* A. Lateral view of left femur; B. Posterior view of right tibia and fibula; C. Ventral view of right pes.

The pelvic girdle and right hind limb are completely preserved, but there is only the femur preserved of the left leg. The ilium is thinly plate shaped and slightly concave laterally. The acetabulum is crescentic and in lateral perspective is funnel shaped. A bony plate that projects

ventrally off the anteromedial side of the acetabulum represents the ossified medial wall. The dorsolateral side of the acetabulum is distinctly thickened to compose a round and smooth supra-acetabular flange (Fig. 5). The anterior lobe of the ilium is long and narrow, and curves ventrally and slightly laterally. The ventral portion gradually rotates anteromedially to facilitate the attachment of the M. pubio-ischio-femoralis internus. The posterior lobe is short and high with the dorsal section rotating first medially and then ventrally to form a distinct lateral depression for the initiation point of the M. caudi-femoralis brevis. The medial side of the ilium is slightly convex. Three sacrocostal nodes are observed.

The pubis is shaped like an inverted V. The prepubis is longer than on *Fabrosaurus*, laterally flattened, and slightly ventrally curved. The obturator foramen is relatively small and triangle-shaped. The posterior pubis is thin, long, straight, and club shaped. It runs along the ventral ischium posteriorly to the posterior end of the ischium. The ischium is long and flat with a broad proximal end. The pubic peduncle is broader and larger than the iliac peduncle. The obturator process is small and situated ventrally on the proximal third of the element. The shaft is slightly curved and rotated with a round and glossy dorsal spine at its midpoint. On the medial side there is a lateral depression. The distal end is broad and flat.

Table 3. Limb Measurements of *Agilisaurus louderbacki* (mm).

Element	Length	Proximal breadth	Distal breadth	Smallest shaft diameter
Right humerus	97.0	21.9	22.3	11.2
Right ulna	85.0	13.2	14.0	7.4
Right radius	87.6	7.5	11.3	5.0
Left femur	198.0	39.5	38.0	26.0
Right femur	199.0	34.5	44.6	23.0
Right tibia	207.0	35.0	47.8	18.4
Right fibula	193.0	20.5	14.2	6.0

The femur is robust with a large head that is nearly perpendicular to the shaft but does not possess a distinct constriction at its neck. The greater trochanter is high and nearly at the same level as the femur head. The lateral side is unevenly concave and convex. The lesser trochanter is situated anteriorly as a subcrescentic-shaped process, is lower than the greater trochanter, and is separated from it by a deep cleft. A well-developed fourth trochanter is characteristically pendent and located posteromedially with an index of 0.43. The shaft is rotated, distinctly anteriorly curved, and subrounded in shape. A small elliptical foramen is present on the lateral side by the fourth trochanter which constitutes a nutrient blood canal. This feature has not been reported on other related taxa. A broadened, elliptical depression lies on the medial side of the shaft to facilitate the attachment of the M. caudi-femoralis longus. The distal end is transversely broadened with a deep and broad intercondylar groove. An anterior trochlea is absent and the medial condyle is slightly smaller than the lateral condyle.

The tibia is robust, long, and straight (Table 3), being 1.04 the length of the femur. Its proximal end is inflated into a triangular surface. The anterior surface is represented by a large cnemial crest for accommodating the fibula. The shaft is hollow and circular in outline with relatively thick walls. The distal end is a distinctly transversely broadened triangle with a concave anterior surface, convex posterior surface, and a swollen ridge at its midpoint. The fibula is long and gracile with a laterally flattened proximal end and a concave medial side for accommodation of the lateral condyle and cnemial crest of the tibia. The shaft is straight and hollow with relatively thin walls. The distal end is transversely flattened to accommodate the anterolateral side of the tibia.

The calcaneum is concave. An anterior tibial process is not well developed but a posterior ascending process is relatively distinct. The astragalus is a multifaceted lenticular element with a concave dorsal surface to accommodate the fibula. The posterior facet is concave for articulation with the tibia. Distal tarsal 1 is ellipsoid and articulates with the astragalus and Mt III. Distal tarsal 2 is relatively thick, semicircular, and articulates with the calcaneum and Mt IV.

Lengths of metatarsals are not equivalent as Mt III is the longest (Table 4), at 52 percent of the femur length. Mt I is reduced, club shaped, and laterally compressed with an inflated distal end. Mt II is shorter than Mt III with a laterally flattened proximal end for the appression with Mt III. The shaft is straight with an inconspicuously swollen distal end. Mt III has a laterally flattened proximal end; its shaft is transversely broadened and slightly curved. Its distal end is slightly inflated with a ligament fossa observable laterally. Mt IV has a transversely broadened proximal end and a distinctly curved shaft that gradually constricts distally. The distal end is slightly inflated. Mt V has been greatly reduced to be thin and stick-like and is appressed against the side of distal carpal 2 and the posteroproximal end of Mt IV. The entire metatarsal series is arched, the posterior surfaces are concave, and in cross-section they are crescentic.

Table 4. *Agilisaurus louderbacki* Right Pes Measurements (mm).

Element	Length	Proximal height	Proximal breadth	Distal height	Distal breadth	Smallest shaft breadth
Mt I	55.0	9.5	3.4	11.0	10.5	5.4
Mt II	92.0	20.4	9.2	12.7	11.8	8.5
Mt III	103.5	17.4	12.6	14.1	18.3	11.8
Mt IV	88.5	13.0	17.0	15.0	14.5	11.8
Mt V	15.8+	—	—	—	—	4.7
Digit I-1	29.5	12.2	9.0	7.8	9.8	6.2
II-1	33.1	14.3	13.6	12.2	12.5	9.6
III-1	32.3	15.5	18.8	11.8	16.0	13.0
IV-1	23.5	12.6	15.4	10.5	12.7	11.0
(ungual) I-2	19.4	10.2	5.8	—	—	6.0
II-2	23.5	13.1	13.0	8.5	11.0	9.8
III-2	26.5	14.4	17.0	10.3	13.9	12.1
IV-1	18.9	12.6	13.3	8.7	12.3	11.5
(ungual) II-2	24.8	10.0	9.8	—	—	—
III-3	22.0	11.9	14.3	8.5	12.3	10.6
IV-3	16.2	10.9	12.0	7.6	11.0	10.8
(ungual) III-4	29.5	9.7	10.6	—	—	—
IV-4	13.6	9.2	9.9	6.7	9.6	9.1
(ungual) IV-5	19.8+	8.2	8.8	—	—	—

Phalangeal formula is 2 3 4 5 with ungual phalanges all clawed. Mt I phalanges are relatively thin and long, while Mt II and III are long and robust. Mt IV phalanges are thick and short. Proximal ends of proximal phalanges are distinctly swollen, concave, and semicircular for articulation with the metatarsals. On the remaining phalanges a slightly swollen medial ridge lies in the center of the proximal ends. Laterally they are slightly concave and their ends are triangular. Medially, they are constricted with slightly swollen distal ends and distinctly concave intercondylar grooves. Ligament fossae on both sides are deep. The clawed unguals constrict to sharp points, curve slightly ventrally, and possess distinct longitudinal grooves on both sides for the accommodation of angular nails.

Discussion and Comparison

1. Phylogenetic position of *Agilisaurus louderbacki*.

Peng (1990) suggested that this taxon is a primitive small ornithischian with skeletal features characteristic of the Fabrosauridae. These include:

a) Dentitions erupt on the margins of the maxillae and mandibles, which is the primary character for the family (Galton, 1972).

b) Dental enamel is thin and complete both lingually and labially; anterior and posterior margins are basically symmetrical, lack well-developed wear facets, and have weakly developed enamel crenellation. These resemble *Fabrosaurus* and are unlike the dentition of *Hypsilophodon*.

c) The fore limb is greatly reduced, hind limb is extended, a supra-acetabular flange is well developed, and there is a distinct M. caudi-femoralis brevis fossa posterior on the ilium. Santa Luca (1984) recognized these as significant postcranial characters for the Fabrosauridae.

d) The femur lesser trochanter lying lower than the greater trochanter and its degree of separation by a deep cleft is one of the reliable characters distinguishing the Fabrosauridae from *Hypsilophodon* (Santa Luca, 1984).

Certain characters are shared with *Hypsilophodon*, including the distinct fossae for cheek musculature, a relatively robust dentary, and several postcranial characters, all of which may be attributed to the intimate relationship between the Hypsilophodontidae and the Fabrosauridae. Here, an assignment to the Fabrosauridae appears more appropriate.

2. Comparison with *Xiaosaurus* and *Yandusaurus*.

Agilisaurus and *Xiaosaurus* share extremely similar skeletal characters attributed to the Fabrosauridae, including leaf-shaped dentition with thin and equivalently thick lingual and labial enamel that lack wear facets, a weakly crescentic lesser trochanter situated lower than the greater trochanter and separated by a deep cleft, and a tibia-femur ratio smaller than 1.10. These express a relatively close relationship between the two, although *Xiaosaurus* appears to be more primitive than *Agilisaurus* with smaller and thinner denticles on the dentition, which lacks dental folds, a relatively straight humerus with an undeveloped deltopectoral crest, inconspicuous anterior curvature of the femur with a fan-shaped projected ridge as the fourth trochanter, shaft lacking nutrient foramen, a tibia with undeveloped cnemial crest and transversely expanded distal end that is distinctly unlike its proximal end, and thin and long limbs. All these differ from *Agilisaurus*. Other fragmentary ornithischian material collected from Dashanpu suggest these characters are all more primitive, and consequently it is believed here that the recognition of independent genera is warranted.

The taxon *Yandusaurus hongheensis* was erected by He (1979) based upon material collected from Hongheba Dam, Zigong (approximately 10 km from Dashanpu). He et al. (1983) described two ornithischian skeletons, T6001 and T6002, from Dashanpu, recognizing principlal characters to be consistent with *Y. hongheensis* but also displaying numerous secondary discrepancies. Consequently, these specimens were assigned to the separate species *multidens.* In actuality, the numerous similarities shared between *Y. multidens* and *Y. hongheensis* listed by He et al. are not significant diagnostic characters. These include a well-developed ventral keel on cervical vertebrae, small triangular cervical spines, and amphiplatyan rectangular dorsal vertebrae with short striations laterally, round and smooth ventral surfaces, and thin plate-shaped neural spines. These characters are symplesiomorphies for all small ornithischians, and as such cannot be applied toward species recognition. Direct comparison of these taxa suggests large discrepancies.

Firstly, although *Y. hongheensis* is a small ornithischian, it is comparatively much larger, with an estimated body length of 3 m, while *Y. multidens* is a much smaller individual at 1 m. Although size discrepancy cannot be regarded as a significant basis for taxonomic assignment, it does represent a certain level of difference between taxonomic groups. Secondly, the maxilla preserved on *Y. hongheensis* has labial enamel thicker than lingual enamel, in addition to well-developed enamel folds and wear facets, which are more similar to the later *Hypsilophodon*. On *Y. multidens* tooth enamel is equivalently thick on both sides, wear facets are not well developed, and dental folds are weakly developed, which are distinctly characteristic of the Fabrosauridae. Thirdly, the humerus of *Y. hongheensis* is distinctly curved with an extremely inflated proximal end and a very well developed deltopectoral crest, expressing its much more derived nature over *Y. multidens*. Obviously, they do not belong in the same evolutionary lineage and it is not appropriate to place them at the same family rank, much less the same genus. *Y. hongheensis* is recognized as a hypsilophodontid while *Y. multidens* is undoubtedly a member of the Fabrosauridae.

Y. multidens and *Agilisaurus* were recovered from the same locality and may be recognized as equivalent taxa. Cranially, they share extremely high maxillae, small lachrymals in contact with prefrontals, antorbital fenestra located anteriorly, and a longitudinal depression at the midpoint of the nasal suture. Dentally they are also similar. They both possess numerous cheek teeth in tight alignment that erupt at the margin of the maxilla with triangular crowns, display basically symmetrical anterior and posterior margins, have thin and equivalently layered enamel, and weakly developed dental folds. Postcranially, ossified tendons are limited to the dorsal and sacral regions, and are absent on the caudals, while scapulae are shorter than humeri, with equivalent ratios. Hind limbs are also equivalent.

Their discrepancies include the smaller skull of *Y. multidens*, its more anteriorly placed orbit, a supraorbital that is not as well developed as on *Agilisaurus*, a central section of the parietal that is not as conspicuously constricted, a laminar supra-acetabular flange, anterior curvature of femur not as noticeable as that of *Agilisaurus*, and a shaft that does not possess a nutrient foramen. Whether or not these discrepancies are due to individual variation must await more advanced work. From the perspective of the numerous shared characters, however, there is no doubt they are congeneric, and consequently *Y. multidens* is reassigned to *Agilisaurus* as *A. multidens*.

3. Comparisons to other related taxa.

Gongbusaurus shiyii was described by Dong, Zhou, and Zhang (1983) on the basis of two isolated teeth collected from the Late Jurassic Upper Shaximiao Fm. at Rongxian Co., Sichuan. Initially the specimens were assigned to the Fabrosauridae. Later, Dong (1989) described a second species *G. wucaiwanensis* from the Late Jurassic Shishugou Fm., in the Kelameili Region of the Junggar Basin, Xinjiang Autonomous Region, and reassigned the genus to the Hypsilophodontidae based upon the eruption of the dentition from the medial side of the dentary. *Gongbusaurus* teeth are very similar to *Echinodon* from Europe, particularly the Xinjiang specimens, which aside from having slightly smaller denticles, a slightly lower tooth crown, and slightly blunter teeth, appear nearly identical to the European form. Moreover, the Xinjiang specimen is represented by two replacement teeth that, due to their placement of eruption, cannot represent functional dentition. Consequently, it is believed here that *Gongbusaurus* is appropriately reassigned to the Fabrosauridae. *Gongbusaurus* shares several similarities with *Agilisaurus*. However, it differs by the presence of closely packed tiny marginal denticles on the premaxillary teeth, a particularly noticeable medial keel on the dentition, and the presence of four small distal carpals.

The Late Triassic or Early Jurassic *Fabrosaurus australis* is the type for the family. Compared to *Agilisaurus* it has a distinctly smaller and lower cranium with a relatively more ventrally placed antorbital fenestra, indistinct buccinator fossae musculature, a low coronoid

process, mandibular foramina, and six premaxillary teeth with relatively few cheek teeth. Its scapula is longer than the humerus, and there are well-developed ossified tendons on the caudal region. Obviously, there is no close relationship to *Agilisaurus* due to the extremely primitive characters on *F. australis*.

Echinodon becklesii from the Late Jurassic-Early Cretaceous transition beds of Europe shares dental characters similar to *Agilisaurus,* but distinctly differs by possessing well developed medial keels, lateral ridges, relatively numerous denticles, and a noticeable diastema between the premaxilla and maxilla.

There are certain shared characters among the Chinese fabrosaurid skeletons known to date that express their close relationship and which indicate an independent derived lineage for the family. From the perspective of geographic and geochronologic distribution, the evolution of this lineage followed the southwest to northeast trending migration of depositional basins.

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