

**A Chinese archaeopterygian, *Protarchaeopteryx* gen. nov.**

by

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## Introduction\*

The discoveries of *Confuciusornis* (Hou and Zhou, 1995; Hou et al, 1995) and *Sinornis* (Ji and Ji, 1996) have profoundly stimulated ornithologists' interest globally in the Beipiao region of western Liaoning Province. They have also regenerated optimism toward solving questions of avian origins. In December 1996, the Chinese Geological Museum collected a primitive bird specimen at Beipiao that is comparable to *Archaeopteryx* (Wellnhofer, 1992). The specimen was excavated from a marl 5.5 m above the sediments that produce *Sinornithosaurus* and 8-9 m below the sediments that produce *Confuciusornis*. This is the first documentation of an archaeopterygian outside Germany. As a result, this discovery not only establishes western Liaoning Province as a center of avian origins and evolution, it provides conclusive evidence for the theory that avian evolution occurred in four phases.

## Specimen description

**Class Aves Linnaeus, 1758**

**Subclass Sauriurae Haeckel, 1866**

**Order Archaeopterygiformes Furbringer, 1888**

**Family Archaeopterygidae Huxley, 1872**

**Genus *Protarchaeopteryx* gen. nov.**

**Genus etymology:** Acknowledges that the specimen possesses characters more primitive than those of *Archaeopteryx*.

**Diagnosis:** A primitive archaeopterygian with claviform and unserrated dentition. Sternum is thin and flat, tail is long, and forelimb resembles *Archaeopteryx* in morphology with three talons, the second of which is enlarged. Ilium is large and elongated, pubes are robust and distally fused, hind limb is long and robust with digit I reduced and dorsally migrated to lie in opposition to digit III and forming a grasping apparatus. Forelimb/hind limb index is 0.7 and proximal metatarsals are fused. Torso feathers are 50 mm in length with short and robust shafts. Tail fan is extremely well developed. Feathers are as long as 150 mm with a slender and elongated shaft and slender and gracile barbs.

***Protarchaeopteryx robusta* gen. et sp. nov.**

**Species etymology:** *Robusta* - Latin for strong and vigorous, in reference to the long and powerful hind limb on the specimen.

**Type:** An incomplete skeleton, Chinese Geological Museum specimen #GMV2125.

**Locality and stratigraphic position:** The first marl in the Upper Jurassic lower Yixian Fm. west of the village of Sihetun, Shangyuanxian, in the municipality of Beipiaoshi, Liaoning Province.

**Species diagnosis:** As for genus.

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**Description:** Skull is poorly preserved and fragmentary, prohibiting an adequate description. Only two teeth are distinctly preserved, one of which is relatively complete, slightly claviform in morphology with a smooth and glossy surface, posterior margin lacks serrations, its diameter is 2.5 mm, and length is 12 mm.

Cervical series is also poorly preserved and thus morphology and count are undetermined. There are four to five vertebrae in the midsection that are ill-defined in outline but indicate a length of 16 mm. Most dorsals are lost and only several vertebrae in the posterior region are preserved, among which are two that are distinct, with lengths of 13 mm and heights of 11 mm. Ribs are not preserved. Sacral vertebrae display a slight degree of fusion. Intermittent sequences of caudals are preserved for a total of 23 vertebrae, although it is estimated the total count would approach 30. Diapophyses are well developed on the anterior and mid-caudals with lengths of 12 mm and breadths of approximately 4 mm.

Only a portion of the sternum is distinct, consisting of a thin and flat margin.

The forelimb, hind limb, and pelvic girdle are completely preserved and quite distinct. A vast majority of the skeleton is pneumaticized and because the specimen has been subjected to compressional distortion, several of the skeletal elements have become flattened and fractured. Thus, the breadths of these elements are probably slightly exaggerated.

The forelimb is extremely similar, both in size and morphology, to those of the Solnhofen specimen of *Archaeopteryx lithographica* (Wellnhofer, 1992), only slightly broader. The right forelimb is completely preserved with a length of 31.0 cm. The right humerus is nearly complete with a length of 8.8 cm. The proximal one-third of the shaft is expanded with a simple convex articular surface, and the distal two-thirds of the shaft is relatively slender. The left radius and ulna are exceptionally complete; both are shorter than the humerus and nearly equivalent in length at 7.2 and 7.4 cm. The radius is relatively straight but the ulna is slightly broader, particularly at its proximal end which is twice the breadth of the radius, and its shaft is posteriorly projected or convex. Faint impressions of three carpals lie on the right side. The ulnare and radiale are small but there is a broad distolateral carpal.

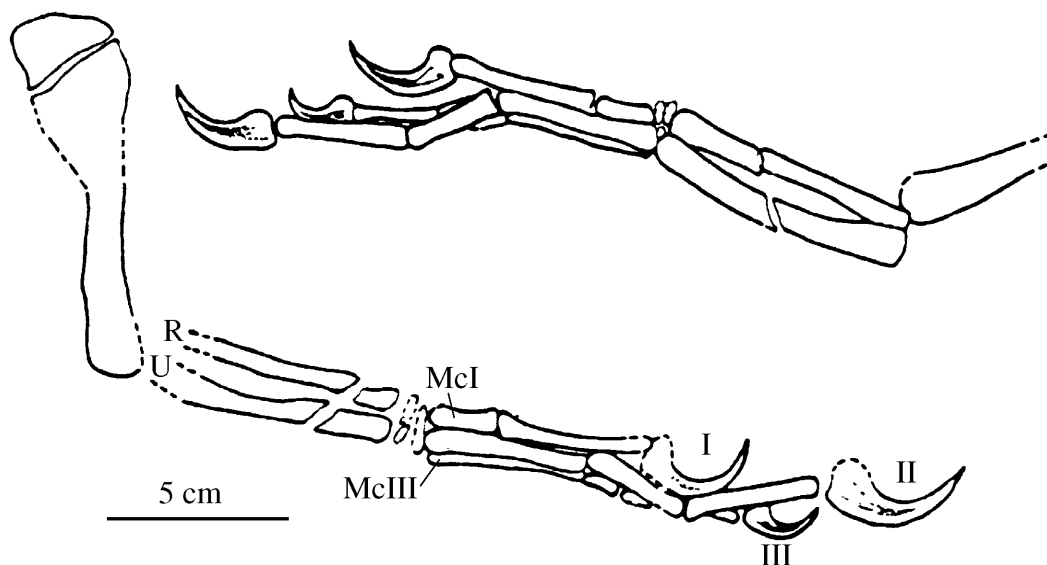
Manus digits on both sides are relatively well preserved but are particularly distinct on the left side. Manus length is 13.5 cm; digit II is the longest and broadest in the series, and digit III is relatively slender. Metacarpal I is short (17 mm), and metacarpals II and III are 44 and 45 mm long respectively, 2.5 times the length of MCI. Digit length indices are extremely close to those of *Archaeopteryx*, but they are slightly broader (Fig. 1). Talons are recurved, acute, and have an inflated base. The talon on digit II is the largest with a length of 36 mm and basal breadth of approximately 10.5 mm. There is a distinct lateral groove on the talons which is broad at the proximal end but narrows and attenuates at the distal end.

The pelvic girdle is robust and forms a fixed yoke with the sacral vertebrae, indicating the ability for vigorous saltation. The ilium is broad and robust; its length slightly exceeds 9.5 cm and its dorsal margin is dorsally convex to form a distinct arc, a morphology extremely close to that of *Sinosauropteryx prima*. The pubes are robust, 8.0 cm in length, with fused termini that do not expand to more than 9 mm anteroposteriorly.

On the hind limb, only the proximal left femur is damaged; the remaining elements are extremely distinct. The right hind limb is 44.0 cm in length, 1.4 times the length of the forelimb.

The femur is extremely long, approximately 12.0 cm, with a slight curvature and an expanded medial side. The distal end is 21 mm in breadth with a pair of articular condyles, and in the midsection the shaft becomes slightly constricted. The tibia is 15.5 cm in length with a nearly planar proximal facet for a tight contact with the proximal fibula. The breadth of both the tibia and

fibula is 25 mm. These elements are relatively straight with breadths generally equivalent to the femur and distal breadths of approximately 19 mm. Tibia is 1.3 times the length of the femur and its walls are approximately 2 mm thick. The fibula is in tight contact with the lateral tibia; distally it gradually becomes extremely slender, and at the midpoint of the tibia it is only 2.5 mm broad. Finally it becomes fused with its lateral counterpart.



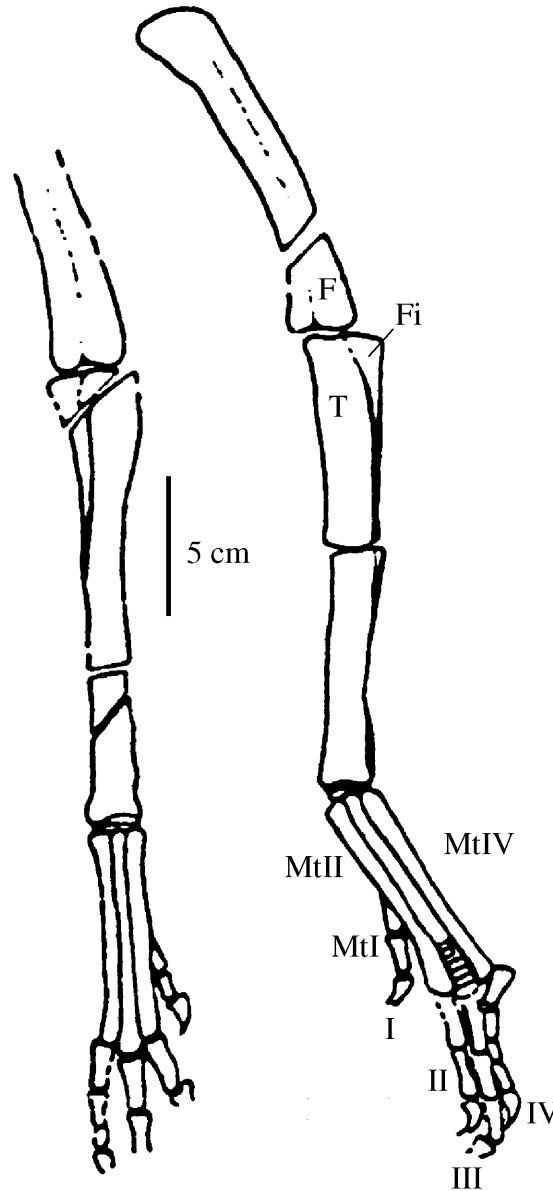
**Figure 1.** Left (A) and right (B) forelimbs of *Protarchaeopteryx rubusta* gen. et sp. nov. (GMV2125) H. Humerus, McI-III. Metacarpals I-III, R. Radius, U. Ulna, I-III. Digits I-III.

Two tarsals are extremely flattened and are not fused to the tibia. The complete length of the pes is 15.5 cm. Metatarsals II-IV are extremely elongated with respective lengths of 7.7, 8.6, and 8.1 cm. They are unfused and their breadths are equivalent. MtI is only 13 mm in length and is situated posteromedial to MtII, lying in opposition to the other three metatarsals. Pes phalangeal formula is 2-3-4-5-0. Digits I and IV have relatively short phalanges but those of digits II and III are relatively elongated. The lengths of the pes talons do not differ greatly from those of the phalanges (Fig. 2).

Feathers are relatively well preserved on the lateral right tibia and proximolateral left femur. Feather lengths generally do not exceed 5.0 cm, the shafts are relatively short and thick, and barbs are slender, as in a typically avian feather. At the end of the tail there is a series of four extremely long feathers 1.5 cm in breadth and preserved lengths of 10.0 cm, although it is estimated these feathers exceeded 15.0 cm in length. The shafts are slender, elongated, and extend directly to the feather termini. Barbs are slender and gracile. Each quill length is 16-18 mm and a sequence of approximately 20 barbs begins to diverge from the shaft 20 mm from the base.

**Comparison:** Comparison to *Sinosauropteryx prima*: In October, 1996, the authors of this text described a primitive bird that was .65 m in length, excavated from the Shangyuan quarries at Beipiao, Liaoning Province, which they named *Sinosauropteryx prima* (Ji and Ji, 1996). In December of that same year, the Beipiao municipal authorities donated another specimen of this species to the Chinese Geological Museum which represented an adult 1.06 m in length. *Protarchaeopteryx* approaches the size of *Sinosauropteryx* (hind limb lengths are nearly equivalent) and its pelvic girdles and hind limbs are extremely robust. However, they are clearly distinct in the following characters: (1) *Protarchaeopteryx* dentition is claviform with a smooth and glossy surface, whereas the dentition of *Sinosauropteryx* is acutely triangular with very weak serrations on its margins. (2) The *Protarchaeopteryx* caudal series is approximately 30 in count but on

*Sinosauropteryx* the tail is extremely long with a count exceeding 50 centra. (3) The *Protarchaeopteryx* forelimb has been modified into a large and elongated limb, while on the latter the forelimb is still relatively short and small. (4) The *Protarchaeopteryx* tail fan is extremely well developed with exceptionally long feathers approximately 15.0 cm in length that have conspicuous shafts. Feathers on *Sinosauropteryx* are more foliate with lengths of 2.3 cm and breadths of 1.1 cm, and they have extremely weak shafts. These two genera are considered to be related; *Sinosauropteryx* represents the more primitive of the two and is ancestral to *Protarchaeopteryx*. Other characters also support *Sinosauropteryx* as a member of the class Aves.



**Figure 2.** Hind limbs of *Protarchaeopteryx robusta* gen. et sp. nov. (GMV2125).  
F. Femur, Fi. Fibula, MtI-IV. Metatarsals I-IV, T. Tibia, I-IV. Digits I-IV.

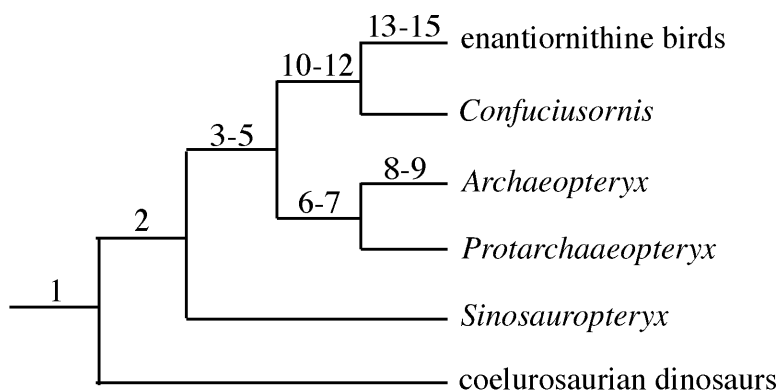
Comparison to *Archaeopteryx lithographica*: To date there have been six complete or partial skeletons of *Archaeopteryx* described. The largest is twice the size of the smallest but is nevertheless retained in the same species. *Protarchaeopteryx* forelimb length and morphology are

basically consistent with those of the largest specimen of *Archaeopteryx* from Solnhofen (Wellnhofer, 1992). Also, the claviform premaxillary dentition of *Archaeopteryx* resembles that of *Protarchaeopteryx*, as do other skeletal morphology and tail feather morphology. However there are noticeable distinctions between the two: *Protarchaeopteryx* teeth are distinctly more robust than those of *Archaeopteryx*, as are the pelvic girdle and hind limb. The former's hind limb/forelimb index is approximately 0.7 but in *Archaeopteryx* the index is generally at parity. *Protarchaeopteryx* metatarsals are unfused but on the latter there is proximal fusion. *Protarchaeopteryx* has approximately 30 centra in its caudal series but in *Archaeopteryx* there are approximately 23 caudals.

Both genera are regarded as at approximately the same evolutionary level due to their similarities in dental morphology, forelimb morphology, extremely well developed tail fan, and feather morphology. These synapomorphies also justify the inclusion of *Protarchaeopteryx* in the family Archaeopterygidae, although it is regarded as more primitive because it has a more elongated tail, more robust pelvic girdle, longer and larger hind limb, and unfused proximal metatarsals.

Comparison to *Confuciusornis sanctus*: Because *Confuciusornis* also possesses three distinct manus talons (Hou et al., 1995), it was initially regarded as the most primitive bird approaching *Archaeopteryx*. The authors of this text have reevaluated several tens of specimens of *Confuciusornis* in detail and believe that the original description of Hou et al. (1995) requires important revisions and supplementary description. *Confuciusornis* is more derived than *Protarchaeopteryx*; it has distinct apomorphies including its modification to a small, gracile, and lightly constructed skeleton, reduced dentition, extremely short caudal series with terminal centra fused into a pygostyle, an oval pneumatocoel on the proximal humerus, and extremely well developed flight feathers.

**Discussion:** Specimens of primitive birds continue to be discovered in western Liaoning Province, supporting the conclusion that the origin of the class Aves occurred in the Jurassic. The genera *Archaeopteryx*, *Protarchaeopteryx*, and *Sinosauropteryx* should be included in the class based upon characters including the presence of feathers and endothermy.



**Figure 3.** Phylogenetic relationship of primitive avian taxa.

Character states: 1. Pneumaticized skeleton, 2. Feathers present, 3. Sternum present, 4. Well developed tail fan, 5. Retrograde pubis, 6. Elongated forelimb or primitive wing with three talons, 7. Claviform dentition, 8. Lightened and gracile skeleton, 9. Fused proximal metatarsals, 10. Shortened tail, pygostyle present, 11. Flight feathers well developed, 12. Dentition reduced, 13. Manus reduced, 14. Carina present, 15. Tibiotarsus present.

The authors of this text earlier advocated four stages of avian evolution as represented by the *Sinosauropteryx*, *Archaeopteryx*, *Confuciusornis*, and enantiornithine stages (Ji and Ji, 1996).

*Sinosauropteryx*, *Protarchaeopteryx*, and *Confuciusornis* were excavated from the same regional stratigraphic section and their stratigraphic relationships are quite distinct. *Protarchaeopteryx* is regarded as a member of the Archaeopterygidae at the same evolutionary stage as *Archaeopteryx*. Its documentation fills a vacancy between *Sinosauropteryx* and *Confuciusornis* and strongly supports the phylogenetic relationships proposed in Figure 3.

*Protarchaeopteryx* is the first member of the family documented outside Germany and further indicates that China was an evolutionary center for early avian evolution.

To date, *Archaeopteryx* is only documented from the Solnhofen limestones. of Bavaria, Germany. The lithology there represents a lagoon limestone that has produced several hundred paleontological specimens with an age assigned to the Jurassic Tithonian Stage (Barthel and Jablonski, 1989). Therefore, the presence of *Protarchaeopteryx* confirms a Late Jurassic age for the Yixian Fm.

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