First Flightless Pterosaur

David Peters

no affiliation

9 Greenfield Court, Saint Charles, MO 63303 USA

Pterosaur fossils have been discovered all over the world [1], but so far no flightless pterosaurs have been reported. Here an old and rarely studied pterosaur fossil (Sos 2428) in the collection of the Jura Museum in Eichstätt, Germany, was re-examined and found to have a reduced pectoral girdle, small proximal wing elements (humerus, radius and ulna), three vestigial distal wing elements, the relatively longest pelvis of any pterosaur and the widest gastralia, or belly ribs. This discovery represents a unique morphology for pterosaurs. The Jura specimen lacked the wing size, forelimb muscularity and aerodynamic balance necessary to sustain flapping flight. It was a likely herbivore.

The fossil (Sos 2428) came to the Jura Museum from the collection of the Bishop's Seminary in Schamhaupten. Its original location was given as the silicified plattenkalk of Schamhaupten, Germany (Upper Kimmeridgian,155-150 million years ago). In the Late Jurassic this pterosaur lived on or near a warm, semi-arid island [2]. Associated fossils from the same horizon include the small theropod, *Juravenator starki* [3].

Sos 2428 was preserved in part and several smaller counterparts lifted from the top of the plate and from the bottom, which reveals more skull material. In the original description [4] several bones were considered missing, including the distal mandible, scapula, coracoid, humerus, radius, ulna, carpus, pteroid, the medial manual digits (I and II), the distal phalanges of digit IV and the distal hind limb. Now only the distal mandible and distal hind limb remain unknown (Fig. 1). Tiny distal wing elements were found curled up between the first and second dorsal ribs (the 9th and 10th post-cranial vertebral ribs (Fig. 1a, b)) in close association and nearly articulated. Atypical for pterosaurs (Fig. 1c-g), the largest of these elements (m4.2) was only the size of a dorsal rib, which is how it escaped detection until now. The others (m4.3, m4.4) were much smaller, mere vestiges. Each distal wing phalanx was at least halved in diameter by mid shaft. A strong curve developed in m4.3 that is

more typically seen in m4.4.

Sos 2428 was considered [4] a variety of *Pterodactylus longicollum* with a skull "slightly smaller" and cervical vertebrae "a little longer." These distinctions were then considered [4] in the range of either individual variation or sexual dimorphism. This specimen has never been included in any prior cladistic analyses. Here the generic distinctions warrant a cladistic analysis and a revision of the nomenclature, subjects to be dealt with in a separate paper.

A related, more primitive, but contemporary and likewise mislabeled *Pterodactylus* specimen is BSt 1911 I 31 (Fig. 1c, g), housed in the Bavarian State Collection for Palaeontology and Geology. It shared with the Jura specimen (Sos 2428) a flat rostrum, elongated neck, similar proportions in fingers I-III and a slender build with wide gastralia. Otherwise this much smaller specimen had proportions more typical of other pterosaurs. It was clearly able to fly with a wingspan 9x longer than the torso. When graphically enlarged to the same glenoid-acetabulum length as Sos 2428 (Fig. 1c, d), the differences between these sister taxa become quite clear. While the skulls were similar in length, in Sos 2428 the neck was slightly longer, the pectoral girdle and the entire wing were much smaller, the torso was somewhat larger and the pelvis was considerably longer and more fully fused. The wing of the Jura specimen (Sos 2428) was half as long with a chord only half as deep on a heavier body compared to the scaled-up version of BSt 1911 I 31. Most other wing and pectoral elements of Sos 2428 were similarly halved in all dimensions. The reconstructed wingspan of Sos 2428 was only 5x the torso length.

Certain other pterosaurs also experienced distal wing phalanx reduction and loss. The University of Nebraska in Lincoln specimen of *Nyctosaurus* (UNSM 93000) had only three wing phalanges with the curved terminal phalanx (m4.3) less than half as long as m4.2 [5]. In this case the hyperelongation of the metacarpus added to a wingspan 18x longer than the torso. The pectoral girdle was robust and the torso was unexpanded. In the azhdarchid, *Quetzalcoatlus* [6], m4.4 was a vestige and the folded wing extended only a short distance beyond the elbow. As in *Nyctosaurus,* the hyperelongation of the metacarpus added to a wingspan 12x longer than the torso and the pectoral girdle was robust. In contrast, the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica in Beijing specimen of another azhdarchid, *Zhejiangopterus linhaiensis* (IVPP V 13397), had similar wing phalanx proportions to *Quetzalcoatlus*, but a wingspan only 8x the torso length [7]. The humerus and other wing elements were relatively slender and short. In this case the pectoral girdle was not robust, but much smaller than the pelvis + prepubis. The pelvis was enlarged to half the torso length. These reductions and modifications would have made *Zhejiangopterus* the weakest flyer among known pterosaurs after the Jura specimen (Sos 2428).

In the Jura specimen (Sos 2428) the more drastic reductions in the wingspan would have further reduced the ability to fly without affecting the ability to travel quadrupedally. In comparison to BSt 1911 I 31, the further lengthening of the pelvis and increased fusion in the sacrum in Sos 2428 indicate that larger stresses were encountered there. While typically quadrupedal while feeding or fleeing, if cornered by a predator or rival into a defensive bluff, this pterosaur with a reinforced pelvis and sacrum could have stood upright, spreading and weakly flapping its clipped wings.

The increase in gastralia width indicates an increase in torso volume. Similar increases in other extinct amniote taxa, such as therizinosaurids, are widely considered to indicate herbivory [8], another behaviour considered atypical for pterosaurs.

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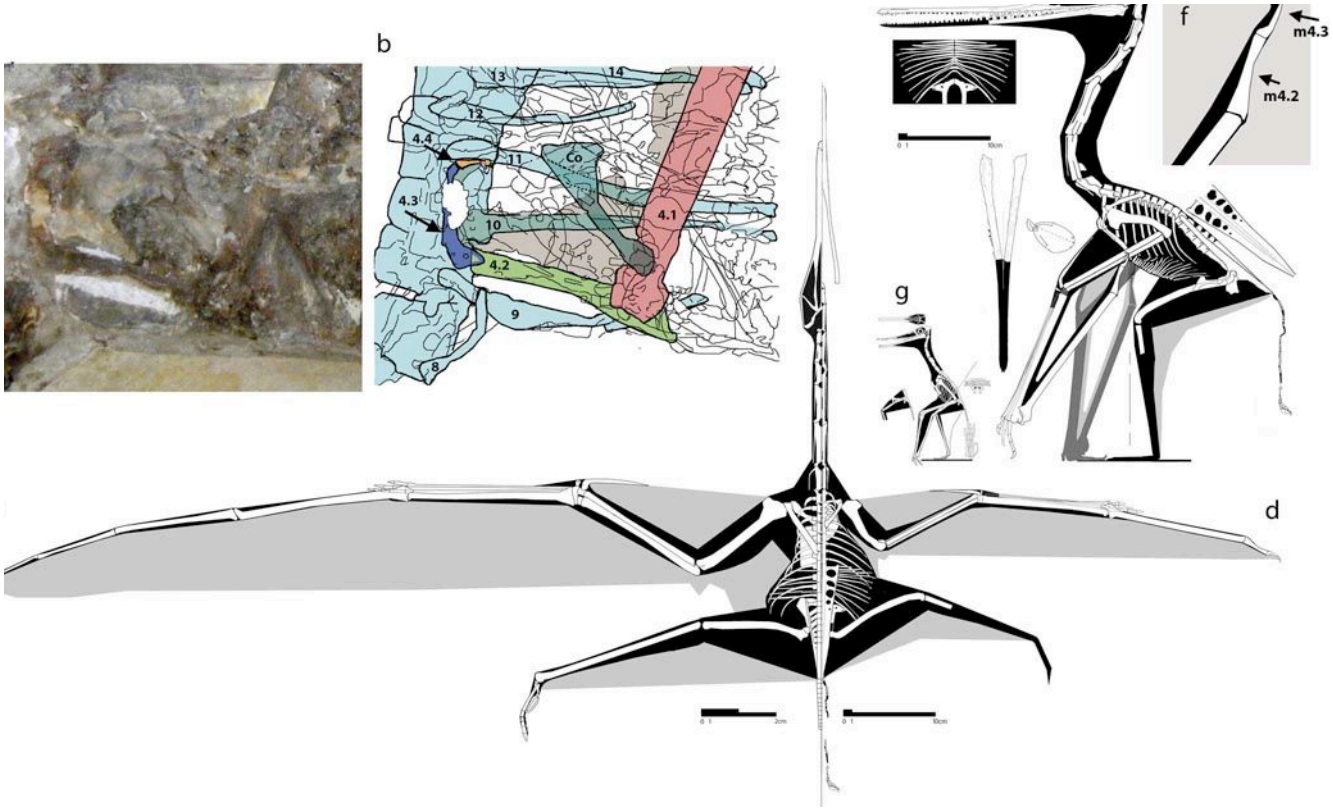
Correspondence and requests for materials should be addressed to D.P. (e-mail: davidpeters@att.net.)

Figure 1. A flightless pterosaur and a smaller flight-worthy relative compared. **a.** Close-up photograph of the Jura specimen (Sos 2428) *in situ*. **b.** Labeled tracing of same. The vertebrae and ribs are light blue and numbered postcranially. The coracoid (co) is in darker blue. The elements of the wing finger are in light red (m4.1), green (m4.2), violet (m4.3), and amber (m4.4). Possible wing membrane material in gray. **c.** Reconstruction in dorsal view of the left half of the Bavarian specimen, BSt 1911 I 31. Scale bar = 2 cm. **d.** Reconstruction in dorsal view of the right half of the Jura specimen, Sos 2428. Scale bar = 10 cm. **e.** Reconstruction of Sos 2428 standing in lateral view, plus the gastralia in dorsal view, the mandibles in ventral view, the sternal complex in dorsal view and the sacrum in dorsal view. **f.** Close-up of the reconstructed distal wing elements of Sos 2428. **g.** Reconstruction of BSt 1911 I 31 standing in lateral view, plus another lateral view of the femur, a dorsal view of the gastralia and a dorsal view of the pes enlarged. Scale bar = 10 cm.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