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SOFT TISSUE IN AN EARLY CRETACEOUS PTEROSAUR FROM LIAONING PROVINCE, CHINA

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ABSTRACT

An Early Cretaceous pterosaur from western Liaoning Province, China shows that impressions of thin, short integument derivatives are densely distributed around the neck of the animal. Four kinds of fibers in the wing are observed, two forms of stiff fibers preserved as groove-like furrows and fine ridges on the margin and the tip of the wing membranes, and two forms of elastic fibers embedded in the interior part of the wing. The fibers show variations in widths from different parts of the wing. Possible blood vessels are found on the same layer with elastic fibers. There are clear integument structures between the toes similar to webs on the feet of wading birds. The wing membranes appear to have connected to the lower part of the leg.

Key words: soft tissues, pterosaur, Yixian Formation, Lower Cretaceous, Liaoning Province of China

INTRODUCTION

Numerous fossil vertebrates found in the Lower Cretaceous Yixian Formation of Sihetun and its peripheral areas of Beipiao City, western Liaoning Province, northeastern China (Swisher et al., 1999; Wang et al., 1998, 1999) have made this region world-famous, matching the fame of the Solnhofen Limestone in Germany. Apart from the great variety of birds found among the fossils discovered so far (Hou et al., 1995, 1999; Hou, 1997; Chiappe et al., 1999), there are also amphibians (Wang and Gao, 1999; Wang, 2000), reptiles (Chen et al., 1997; Ji et al., 1998; Xu et al., 1999; Gao et al., 2000; Norell et al., 2002) and mammals (Hu et al., 1997; Ji et al., 1999). Four kinds of pterosaurs have been reported from the Yixian Formation (Ji and Ji, 1997, 1998; Unwin et al., 2000; Wang and Lü, 2001), with soft tissue impressions reported from one (Wang et al., 2002).

The study of pterosaur soft tissues can be traced back to the 19th century. Goldfuss (1831) was the first to report the tufts of soft tissue in a specimen of *Scaphognathus crassirostris.* Subsequently different terminologies have been applied to the soft tissue or impressions of the wing membrane and skin. They include stitch-like pits in *Rhamphorhynchus* (Wanderer, 1908), striae and striations in the wing membrane of *Anurognathus* (Abel, 1925), wooly fur (Döderlein, 1923), hair (Wiman, 1925; Broili, 1927; Leich, 1964; Sharov, 1971; Wellnhofer, 1975; Bakhurina and Unwin, 1995a), stiffening rods (= Aktinofibrillen; Wellnhofer, 1987), and fibers (Campos et al., 1984; Padian and Rayner, 1993a, b; Wild, 1993; Unwin and Bakhurina, 1994; Bakhurina and Unwin 1995b; for a historical review see Frey and Martill, 1998). Some structures were originally regarded as wrinkles (Pennycuik, 1986, 1988, 1990), but those studies are now questioned (Padian and Rayner, 1993a). Martill and Unwin (1989) analyzed wing membrane from an unidentified Cretaceous pterosaur from Brazil with an SEM, but the identification of the soft tissue as wing membrane was challenged (Kellner, 1996; Frey and Martill, 1998). Wang et al. (2002) described a beautifully preserved specimen of *Jeholopterus ningchengensis* from the Early Cretaceous of China with wing membrane, "hairs", and interdigital webs preserved.

Recently, partial remains of a well-preserved pterosaur lacking the skull were discovered at Liaoning (Lü and Wang, 2001). As documented and interpreted below, soft tissue impressions associated with the skeleton are clearly seen under light magnification (Figs. 1, 3-4), and the structure of the soft tissues was investigated using a scanning electron microscope.

DESCRIPTION

The skeleton (Beipiao Paleontological Museum, BPM 0002)

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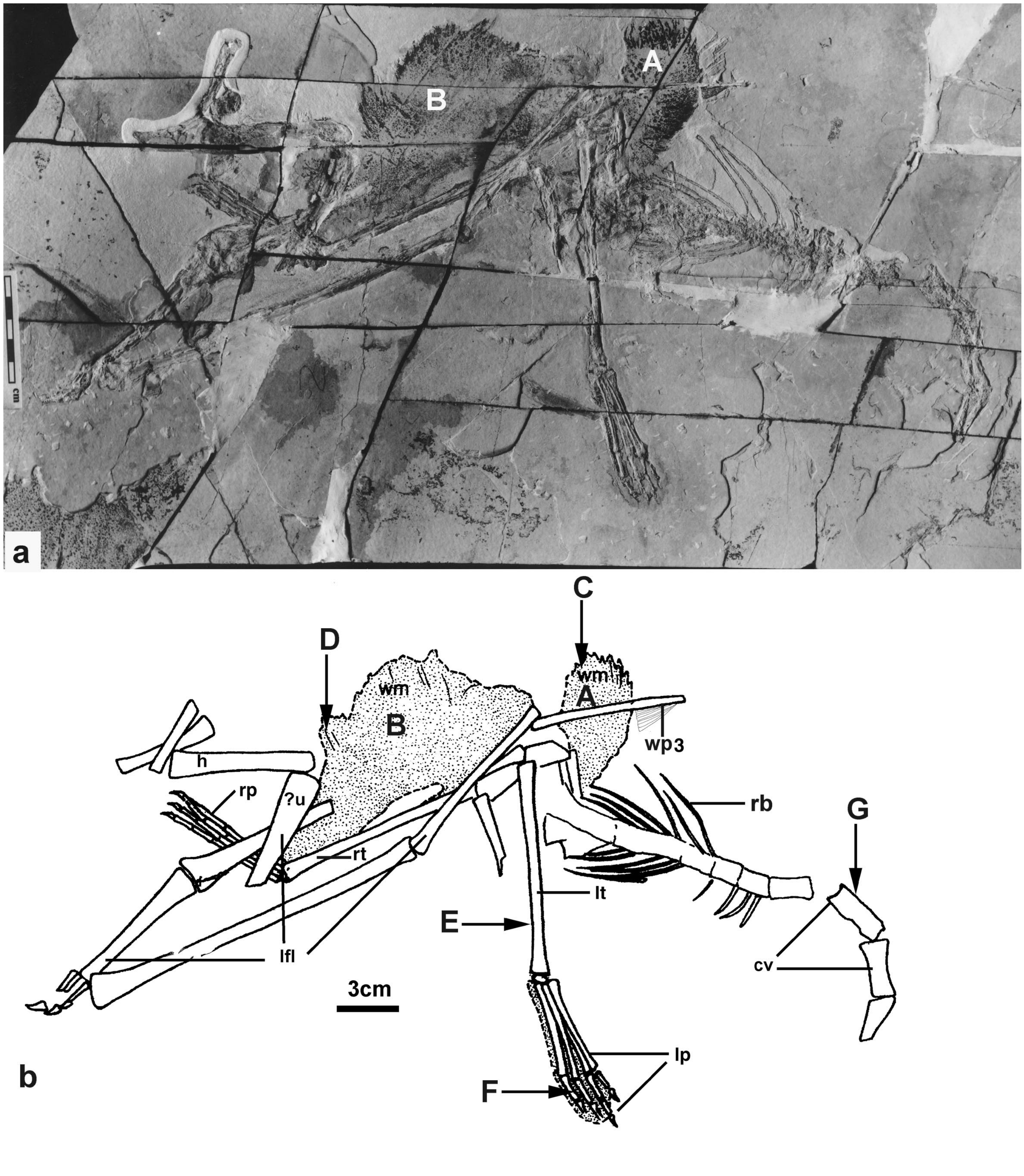


FIGURE 1. General disposition of the skeleton of a pterosaur with a distinct wing membrane impressions (BPM 0002), photograph (**a**), Areas A and B are shown in detail in Fig. 3, and drawings (**b**), showing the positions sampled for SEM micrographs. Scale bar = 5cm in **a**. **Abbreviations: cv**, cervical vertebrate; **lfl**, left front limb; **lp**, left pes; **lt**, left tibia; **rb**, ribs; **rt**, right tibia; **rp**, right pes; **wm**, wing membrane; **wp3**, the third wing phalanx. **A** and **B** are enlarged in Fig. 3 and 4, **C-G** are the positions of samples used for SEM micrographs.

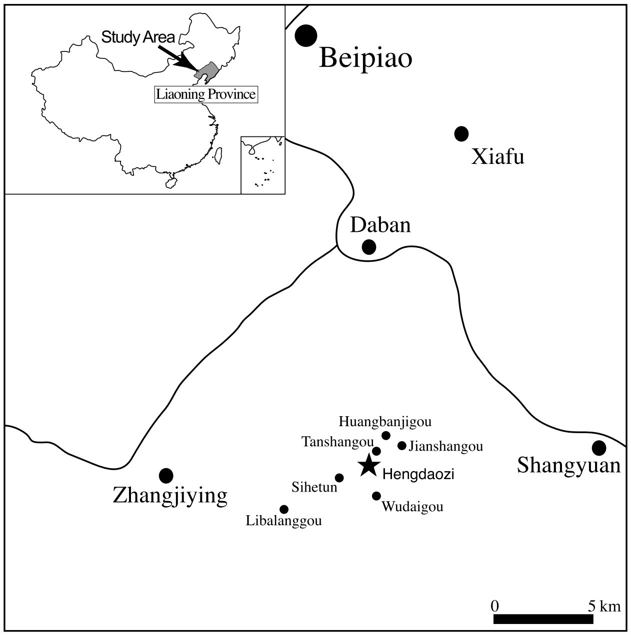


FIGURE 2. Map of the fossil locality.

is incomplete, but well-preserved (Fig. 1). It was found in the 8th layer of the Yixian Formation (Wang et al., 1998, 1999) at Hengdaozi, Tanshan Gou, near Sihetun in Beipiao City (Fig. 2). The specimen is preserved on the bedding plane of a slab of fissile siltstone. Four cervical vertebrae, at least 14 dorsal vertebrae, seven dorsal ribs, a nearly complete left forelimb, and distal parts of both legs are preserved. Soft tissue (Fig. 1) is preserved as integumentary derivatives in the neck region, as wing membrane near the tip of third left phalanx and in two other areas of the wing (Figs. 3, 4), as muscle tissue remnants along the left tibia, and as webbing between the left pedal digits. Samples suitable for SEM analysis are present in the following areas: (1) the lateral surface of the cervical vertebrae (Fig. 1b: G); (2) the outer margin of the wing membrane (Fig. 1b: C, D); (3) adjacent to the tibia (Fig. 1b: E), and (4) between the digits of the pes (Fig. 1b: F).

The integument impressions near the neck consist of thin, short fur-like structures (0.24µm in diameter, 4µm in length; Table 1) arranged in clusters and oriented with the long axis outward from the neck (Fig. 5A). The clustered arrangement is distinct from the ordered and regular arrangement of muscle fibers. These structures are also shorter and narrower than muscle fibers seen along the tibia and do not exhibit banding. Tissue preserved near the tibia displays regular banding (Fig. 5H) characteristic of muscle fibers (Martill et al., 1990). There is a thin wrinkled layer of integument between the digits of the left pes (Fig. 5B), demonstrating that this pterosaur had webbed feet. The surface viewed with SEM is rough and irregular, suggesting it may represent stratum corneum.

The wing (Fig. 1) is only partially preserved and therefore the complete outline cannot be determined, although its tip and connection with the right tibia can be discerned. The distal region of the left wing membrane is connected to the third phalanx and approaches proximally a portion of wing tissue, which appears to include a segment of the wing margin (Fig. 1a: A). A third portion of wing (Fig. 1a: B) also preserves a segment of the margin; however, the fiber direction near the margins in A and B differ. Wing portion B is from the right wing because it connects to the right tibia. Wing portion A, which lies on a slightly different plane from wing portion B, is either the obverse of the wing represented by A, or it is from the left wing. No details of cell structure on the surface of the wing were discerned with SEM; however, the wing membrane exhibits a number of types of elongate structures as ridges and grooves visible with both SEM and light microscope. The structures differ in diameter, shape, and distribution in the wing.

The proximal part of the third wing phalanx (wing spar) lies on the wing membrane. The elongate structures (Fig. 3b: y; Fig. 4b: isf) in the membrane near the third phalanx are straight, closely packed, and aligned nearly parallel to the bone. Because each structure is straight rather than curved, they are interpreted to be stiff and inelastic fibers. The diameter of these stiff fibers is 155 µm, greater than the diameter of fibers in other parts of the wing (Table 1), suggesting that the tip of the wing was reinforced with the strongest fibers.

Near the margin of the wing membrane (Fig. 1b, D), several deep groove-like impressions are radially arranged on the same plane (Fig. 5D: isf). The grooves are greater than 100 µm in

TABLE 1. Measurements of the elongate structures (µm).

Structure	Diameter	Length
Stiff fiber near the wing tip	155	12000
Stiff fiber near the outer margin of the wing	1.47	>100
Elastic fiber near the inner part of the wing	24	>10000
Elastic fiber located in the same layer with blood vessels	0.8	<30
Hair-like structure near the neck region	0.24	4
Blood vessel	<2.5	>200

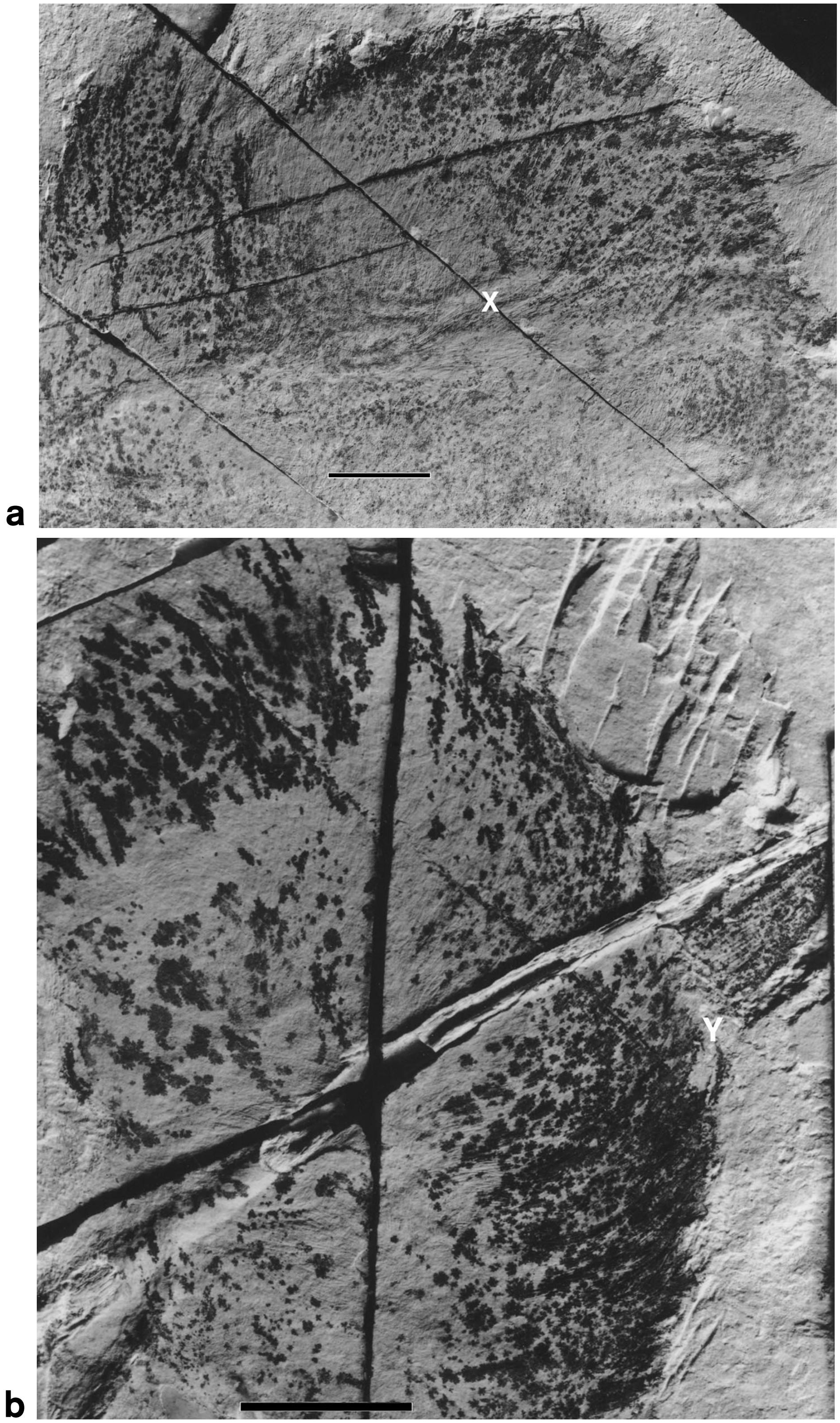


FIGURE 3. **a**. Details of wing membrane (B) preservation in a pterosaur (BPM 0002). **b**. Details of wing membrane (A) preservation in an unnamed pterosaur (BPM 0002). Scale bar = 1cm. A and B are enlargement areas in Fig.1.

length and 0.147μm in diameter. The distance between impressions is 2.81 μm. They are straight and do not overlap, suggesting that they represent stiff, inelastic fibers but are of narrower diameter (Table 1) and different arrangement from those at the wing tip.

As seen with the light microscope, curved elongate structures that cross each other are interpreted here as elastic fibers (Fig. 4a). Each fiber is 24 μm in diameter (Table 1). Seven or eight such fibers are present in the width of 1000 μm (Figs. 3a, 4a). The elastic fibers are not found near the wing margin. A second set of elastic fibers distinguished by smaller diameter (length < 30 μm, diameter = 0.8 μm) is visible under SEM magnification (Fig. 5G: ef).

Among the elastic fibers are curved strand-like structures (>200 μm long, <2.5 μm in diameter), including one with two branches. These structures are different in shape and size from both stiff fibers and elastic fibers. The core of one of the strand-like structures is exposed and appears dark (Figs. 5F, 5G), suggesting that the structure was hollow. Thus, these structures are inferred to represent blood vessels (Figs. 5F, 5G: bv). Small-diameter elastic fibers are found on the same plane with the sparse blood vessels.

Disc-like masses (diameters ≈ 50 μm) with sharp margins (Fig. 5C: bip) occur near the pes region. Smaller spherical structures with diameters less than 10 μm may represent bacteria (Fig. 5E). Additional spherical masses (7 μm in diameter) are densely distributed on the wing membrane. Their surfaces are irregular and pierced with small holes.

DISCUSSION

The shape of the flight apparatus in pterosaurs is still a point of issue (Unwin and Bakhurina, 1994). One hypothesis reconstructs narrow and stiff wings, which did not connect to the hind limb, a bird-like reconstruction (Wellnhofer, 1975; Padian, 1983b, 1988; Padian and Rayner, 1993a), a second reconstruction posits a broad wing that connected front and hind limbs, a bat-like reconstruction (Pennycuick, 1986, 1988). These opinions are still controversial (Alexander, 1994; Peters, 1995; Unwin and Bakhurina, 1995; Unwin, 1999). The wing membrane of the BPM 0002 attached to the tibia near the ankle, similar to that in *Jeholopterus* (Wang et al., 2002), which shows a bat-like arrangement.

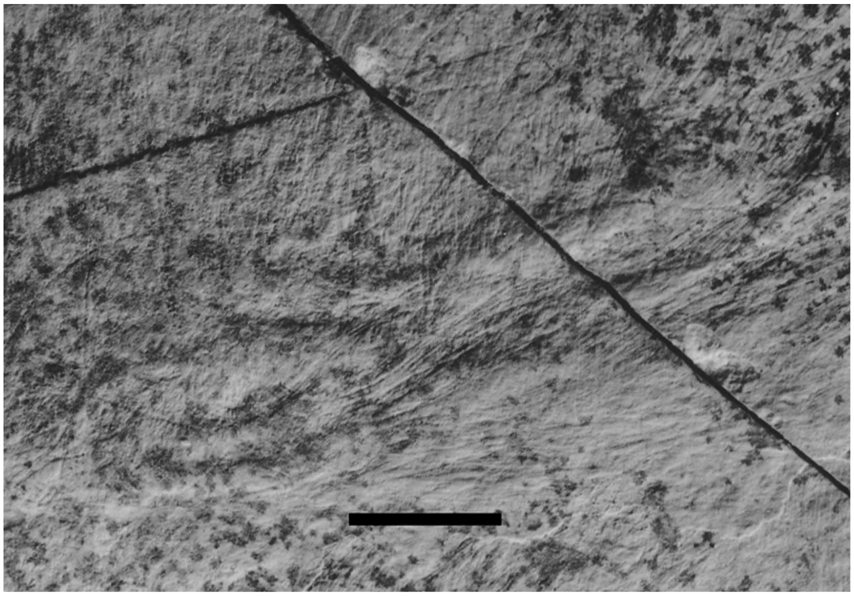
The specimen, although generally little disturbed, exhibits some crumpling of the wing membrane. The crumpled part of the wing may have resulted from the settling of the carcass before it was buried. Black, probably carbonaceous residue that appears near the margin of the wing membrane of BPM 0002 is similar in appearance to that in *Sordes* from Kazakhstan (Bakhurina and Unwin, 1995b).

Two models of wing construction (Martill et al., 1989, fig. 3. b, c) have been put forward, based mainly on impressions from the Late Jurassic Solnhofen Limestone of Germany. Wellnhofer (1975) and Padian (1983a) argued that wing membranes contain stiff fibers that extended transversely. By contrast, Pennycuick (1986, 1988) argued that wing membranes are thin and highly flexible, the interior portion containing elastic fibers but lacking stiff fibers. The SEM micrographs of the wing membrane of BPM 0002 show both stiff and elastic fibers. Stiff fibers probably functioned in supporting the wing membrane. A significant character of the wing fibers is the variation in width from different parts of the wing (Table 1), unlike in other pterosaurs. In *Sordes*, the fibers are about the same width through the wing membranes (Unwin, personal communication, 2001).

The short, clustered, hair-like structures seen under SEM in the neck region of BPM 0002 are clearly distinct from the stiff wing-fibers, which are longer and thicker. They are also different from the hair-like structures in *Eudimorphodon ranzii*, which appear as parallel striae (Wild, 1993) rather than clusters. The fiber impressions near the wing tip appear as strips running nearly parallel to the third wing phalanx (the wing spar). These strips of fiber impressions are straight and closely packed. This is similar to interpretations of the Zittel wing (Padian and Rayner, 1993a, b) and to the structural fibers in the wing tip of *Sordes pilosus* (Unwin and Bakhurina, 1994).

Two portions of the wing membrane (A and B in Fig. 1) proximal to the tip exhibit fiber impressions, but the fibers seem to be more widely spaced and are clearly less regularly aligned than in the small section of membrane from the wing tip shown in Fig. 4a. As shown in Fig. 1, area A lies next to the left leg and the left side of the body. The orientations of fibers in area A are similar to those of *Sordes* in the homologous region of the wing membrane. The angle between the femur and the body suggests that area A may be close to its original position. The wing membrane in area B appears to run down the external margin of the right tibia as far as the ankle. This is similar to the wing in *Sordes*, and the orientations of the fibers are also similar (Unwin, personal communication, 2001). The long, deep, groove-like and radially arranged impressions near the margin of the wing membrane are similar to the “Aktinofibril” described by Wellnhofer (1987), or to the stiff fibers in the outer half of the wing described by Unwin and Bakhurina (1994). The fine, strand-like fibers from the inner part of the wing membrane are not as straight as the fibers from the wing tip. Seven or eight such fibers per mm (Figs. 3a, 4a), are more than seen in the Zittel wing (four or five fibers per mm, Padian and Rayner, 1993a). The curved elastic fibers found on the same level with the blood vessels (Fig. 5G: ef) are direct evidence of elastic fibers embedded within the internal part of the wing membrane.

Muscle fibers preserved near the tibia display regular banding (Fig. 5H). This is similar to that observed in a pterosaur from the Santana Formation, Brazil (Martill et al., 1990). Martill et al. (1990) regarded the striated muscle fibers as from the wing membrane. Kellner (1996) restudied the same specimen and argued that the muscle fibers are not related to the wing a



b

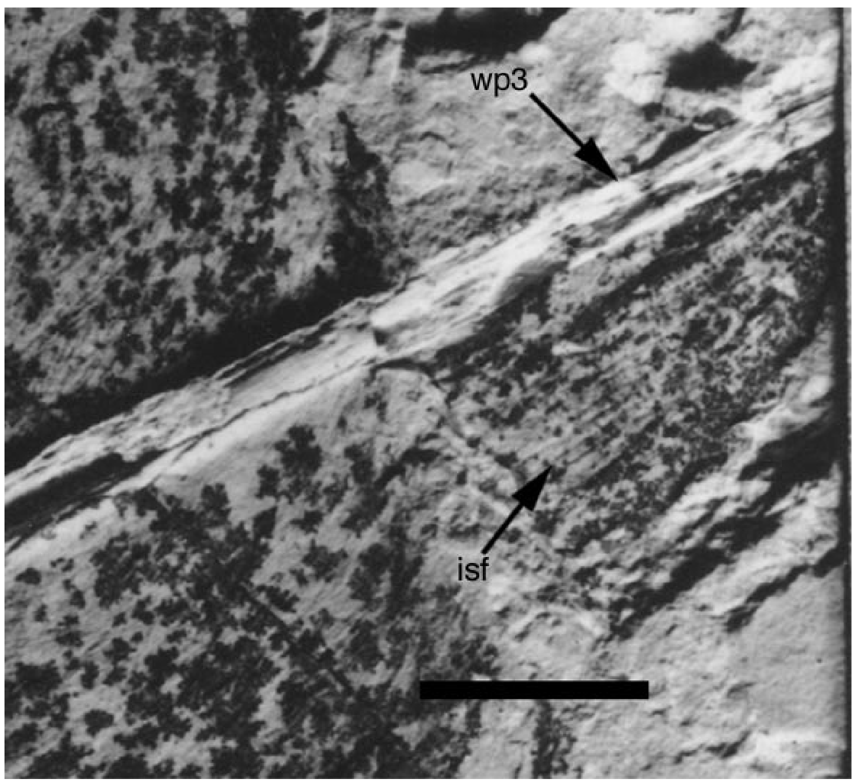


FIGURE 4. **a**. Enlargement of area X in Fig. 3a. Elastic fibers may be covered by the wing skin. **b**. Enlargement of area Y in Fig. 3b, showing the third wing phalanx (wp3) and the impression of stiff fibers. Scale bar = 5mm.

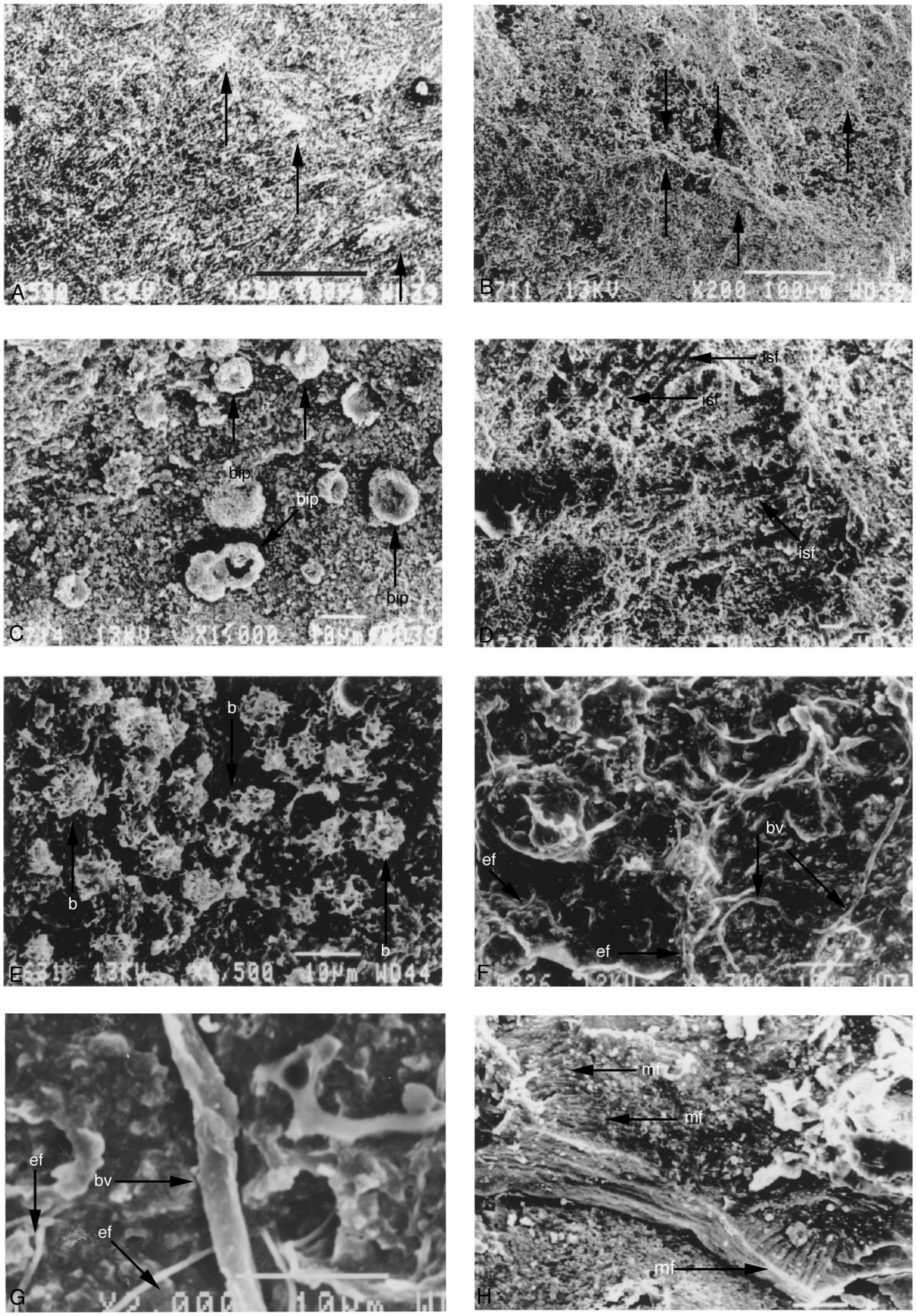


FIGURE 5. SEM micrographs from the locations shown in Fig. 1b. **A**. Adjacent to the neck, arrows indicate the cluster-like impressions of hair-like integumentary derivates, scale bar = 100 mm. **B**. Web impression between the pes digits, arrows indicate partially wrinkled stratum corneum, scale bar = 100 mm. **C**. Bacterially induced precipitates (bip) near the right pes, scale bar = 100 mm. **D**. Structure of the margin of the wing membrane, showing impressions of stiff fibers (isf) from within the wing membrane, scale bar = 10 mm. **E**. Possible spheroid-shaped bacteria (b), scale bar = 10 mm. **F**. Blood vessels (bv) and elastic fiber (ef) from within the wing membrane, scale bar = 100 mm. **G**. Enlargement of **F**, scale bar = 10mm. **H**. Muscle fibers, scale bar = 10 mm; **Abbreviations: ef**, elastic fibers; **b**, bacteria; **bip**, bacteria induced precipitates; **bv**, blood vessel; **mf**, muscle fibers; **isf**, impression of stiff fiber.

membrane. The muscle fibers near the tibia of BPM 0002 supports Kellner's interptretation.

The specimen preserves a web between pes digits, similar to that of modern wading birds. The clearly wrinkled part of the soft tissue around the pes digit area indicates that this area was disturbed before burial.

Smaller spherical structures are interpreted as bacteria. These (Fig. 5E) are similar to those reported from Early Cretaceous fish of the Santana Formation from Brazil (Martill, 1988). In shape and size, the larger disc-like masses with sharp margins (Fig. 5C: bip) near the pes are similar to bacterially induced aragonite and calcite crystal bundles (Buczynski and Chafetz, 1991). The mineralogy of the crystal bundles in this case has not determined.

SUMMARY AND CONCLUSION

Scanning electron micrographs show that different soft tissue structures are found in different body positions in the Liaoning pterosaur BPM 0002. Thin, short fur-like structures are arranged in clusters near the neck, indicating that this animal had hair-like integumentary derivates, at least around the neck area. This may be direct evidence that it was a warm-blooded animal (Alexander, 1994). Stiff fibers lie near the tip and the margin of the wing, and elastic fibers lie near the inner part of wing. Possible blood vessels and bacteria are also found in BPM 0002. The preserved soft tissue near the right tibia shows that the wing membrane connected to the ankle in a bat-like arrangement.

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