

quencies (Fig. 2c). Fluctuations in sap flow at the top and base of a tree are coherent for frequencies less than 0.01 Hz, but at higher frequencies this coherence declines significantly because the tree stem acts as a low-pass filter. A consequence of the coherence between tree transpiration and large-scale turbulent fluctuations of  $q$  and  $T$ , is that as eddies sweep across a forest, sap flux varies in a correlated manner among neighbouring trees (Table 1), creating an invisible analogue to fields of grain rippling in the wind. The correlation coefficients decrease, however, between and among trees lower in the canopy, suggesting that most turbulent gusts do not penetrate through the tree canopy<sup>13</sup>. This demonstrates one way that forest structure affects  $\Omega$  and evaporation.

We have demonstrated that the impact of atmospheric turbulence extends across the leaf-air boundary layer to affect the mass transport of water in trees. This finding contrasts with diffusive or active transport models of water flow in plants<sup>14</sup>. There are several important implications of a chaotic component to water transport in the soil-plant-atmosphere continuum. Because stomata respond to changes in transpiration<sup>15,16</sup> and this nonlinear response is both asymmetrical (closing is more rapid than opening) and overlaps the frequency of displacement events<sup>11</sup>, the intensity and frequency of atmospheric turbulence may provide a previously unrecognized source of feedback that affects stomata and plant functioning. High-frequency variation in transpiration flux will lead to a similar variation in xylem pressure potential that may potentially influence protein synthesis in the roots or at other sites remote from the foliage. Hydraulic pressure fluctuations have been linked with plant electrical action potentials and these action potentials with changes in

protein production<sup>17-19</sup>. Plants respond asymmetrically and non-linearly to high-frequency variations in light<sup>20</sup>. We regard the turbulent nature of atmospheric transport to be as important for plant processes as the response to fluctuating light. □

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- Shukla, J., Nobre, C. & Sellers, P. *Science* **247**, 1322-1325 (1990).
- Bonan, G. B., Pollard, D. & Thompson, S. L. *Nature* **359**, 716-718 (1992).
- Monteith, J. L. *Soc. exp. Biol.* **19**, 205-234 (1965).
- McNaughton, K. G. & Jarvis, P. G. in *Water Deficits and Plant Growth* Vol. VII (ed. Kozlowski, T. T.) 1-43 (Academic, New York, 1983).
- Gao, W., Shaw, R. H. & Paw, U. K. T. *Boundary-Layer Meteorol.* **47**, 349-377 (1989).
- Bergström, H. & Höglström, U. *Boundary-Layer Meteorol.* **49**, 231-263 (1989).
- Finnigan, J. J. & Raupach, M. R. in *Stomatal Function* (eds Zeiger, E., Farquhar, G. D. & Cowan, I. R.) 385-430 (Stanford University Press, Stanford, 1987).
- Martin, P. *Agric. For. Met.* **49**, 45-53 (1989).
- Köstner, B. M. M. *et al. Oecologia* **91**, 350-359 (1992).
- Raupach, M. R., Finnigan, J. J. & Brunet, Y. *Fourth Australasian Conference on Heat and Mass Transfer 75-90* (Christchurch, New Zealand, 1989).
- Grantz, D. A. & Zeiger, E. *Plant Physiol.* **81**, 865-868 (1986).
- Gates, D. M. *Biophysical Ecology* (Springer, New York, 1980).
- Denmead, O. T. & Bradley, E. F. in *The Forest-Atmosphere Interaction* (eds Hutchinson, B. A. & Hicks, B. B.) 421-442 (Reichel, Dordrecht, Holland, 1985).
- Zimmermann, U. *et al. Phil. Trans. R. Soc. Lond. B.* **341**, 19-31 (1993).
- Nonami, H., Schulze, E.-D. & Ziegler, H. *Planta* **183**, 57-64 (1990).
- Mott, K. A. & Parkhurst, D. F. *Plant Cell Environ.* **14**, 509-515 (1991).
- Malone, M. & Stankovic, B. *Plant Cell Environ.* **14**, 431-436 (1991).
- Malone, M. *Planta* **187**, 505-510 (1992).
- Wildon, D. C. *et al. Nature* **360**, 62-65 (1992).
- Pearcy, R. W. & Pflüsch, W. A. in *Ecophysiology of Photosynthesis* (eds Schulze, E.-D. & Caldwell, M. M.) 343-359 (Springer, Berlin, 1994).
- Kelliher, F. M. *et al. Agric. and For. Met.* **62**, 53-73 (1992).
- Hollinger, D. Y. *et al. Ecology* **75**, 134-150 (1994).
- Carter, G. C. & Ferris, J. F. in *Programs for Digital Signal Processing* (eds Digital Processing Committee) 2.3-1 to 2.3-18 (IEEE Press, New York, 1979).

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## *Sordes pilosus* and the nature of the pterosaur flight apparatus

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It is now generally accepted that pterosaurs, Mesozoic reptiles, were true fliers, but the nature of their flight apparatus is still much disputed. Evidence has been presented in favour of bird-like reconstructions with narrow, stiff wings free of the legs<sup>1-6</sup> and bat-like reconstructions with extensive wings incorporating both fore and hind limbs<sup>7-10</sup>, but the Solnhofen Limestone pterosaurs, upon which these models are based, are not sufficiently well preserved to resolve these conflicting interpretations. Here we present a new model, founded on *Sordes pilosus* from the Jurassic of middle Asia (ref. 11, and N.N.B. and D.M.U., manuscript submitted), in which exceptionally well preserved wing membranes show that the hind limbs of pterosaurs were intimately involved in the flight apparatus; connected externally to the main wing membrane and internally by a uropatagium, controlled by the fifth toe. *Sordes* also reveals that, uniquely among flying vertebrates, pterosaurs had a structurally non-homogenous flight surface with a stiffened outer half and a softer, more extensible inner region.

The Upper Jurassic Karabastau formation (Oxfordian-Kimmeridgian) of Karatau in Kazakhstan<sup>12</sup>, a sequence containing very fine-grained lake deposits, has yielded many exception-

ally well preserved fossils<sup>13</sup>; including insects, fish, turtles, a salamander, lizard, crocodile and two pterosaurs: *Batrachognathus volans*, a small insectivore<sup>14,15</sup>, and *Sordes pilosus*, a long-tailed piscivore with a wingspan of 0.65 m (ref. 11, and N.N.B. and D.M.U., manuscript submitted). *Sordes* is represented by seven specimens, varying in completeness, but often naturally articulated, and exhibiting little evidence of post-mortem disturbance. The wing membranes, preserved as high-fidelity impressions picked out by dark, mineralized soft tissues (Fig. 1a) are complete, their edges easily traceable (Fig. 1b), and, in some cases, very fine internal structures such as the individual strands of wing fibres, each less than 10 µm in diameter, are clearly visible (Fig. 2a, b). Wing preservation is substantially better than in Solnhofen pterosaurs, but three-dimensional structures, as reported in a pterosaur wing from the Cretaceous of Brazil<sup>16</sup> have not been found.

As in other pterosaurs, there is a small, triangular propatagium located in the angle of the humerus and forearm, and manipulated by a wrist bone, the pteroid (Fig. 3). The main wing membrane (cheiropatagium) is attached to the rear edge of the forelimb, to the body wall from the shoulder to the hip and to the anterior margin of the hind limb as far as the ankle (Fig. 1a, c). Attachment of the cheiropatagium to the leg has also been reported in *Pterodactylus*<sup>9</sup>, but the exact extent, whether to the knee or to the ankle, is disputed. Some<sup>4,6</sup> restrict it to the thigh, but others<sup>7,9</sup> argue for a more extensive attachment, an idea supported by two examples of *Pterodactylus*<sup>17,18</sup>, in which impressions of the cheiropatagium are preserved adjacent to the lower leg. Elsewhere, wing impressions are rather ambiguous, or not preserved at all, but morphometric studies<sup>19</sup> have revealed a strong correlation between wing and leg length in pterosaurs. A similar correlation occurs in bats where the fore and hind limbs are connected by the flight apparatus, but not in birds in which these structures are physically and functionally independent. In the absence of evidence to the contrary we conclude that attachment of the cheiropatagium to the hind limb was probably universal in pterosaurs.

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The existence of a uropatagium in pterosaurs has been strongly doubted<sup>3-6,9</sup>, but such a structure is clearly evident in *Sordes* (Fig. 1a, b). It attaches to the inner side of the leg as far as the ankle and is supported along its rear margin by the elongate clawless fifth toe (Fig. 1c, d). The tail is displaced to the left, but the membrane beneath it is undisturbed, confirming Sharov's observation<sup>11</sup> that the uropatagium lay below and free of the tail. Fine fibres, extensively distributed within the cheiropatagium, are also present in the uropatagium (Fig. 2a), demonstrating that it too is a flight membrane and not, as some have suggested<sup>6</sup>, a displaced sheet of skin.

What appears to be a small uropatagium is preserved in some examples of *Pterodactylus*<sup>9,20,21</sup> but direct evidence of this flight surface seems to be lacking in other pterosaurs. However, in many rhamphorhynchoids and early pterodactyloids the hindlimbs of articulated specimens often show a comparable positioning to that seen in *Sordes*: the femur is almost perpendicular

to the spinal column and pronated forward 90°, the anterior surface of the crus faces laterally, and the fifth toe is reflected medially (Fig. 3). This is a most unusual attitude for a tetrapod hindlimb and results from its association with a uropatagium which, with the possible exception of derived pterodactyloids, appears to have been present in many pterosaurs.

The close correlation between skeletal morphology and development of the flight patagia in *Sordes* (Fig. 3) means that reconstructions of the wings in other pterosaurs can now be attempted, even where evidence of soft tissues is not preserved. Preservation of fine internal detail in the flight membranes of *Sordes* also shows that the wings of this and, presumably, other pterosaurs were structurally non-homogenous. The outer half of the wing, filled by long, straight, closely packed fibres (Fig. 2c) seems to have been stiff and relatively inelastic, whereas adjacent to the body the fibres are shorter, more sinuous and loosely packed (Fig. 2a), indicating that the propatagium, uropatagium and

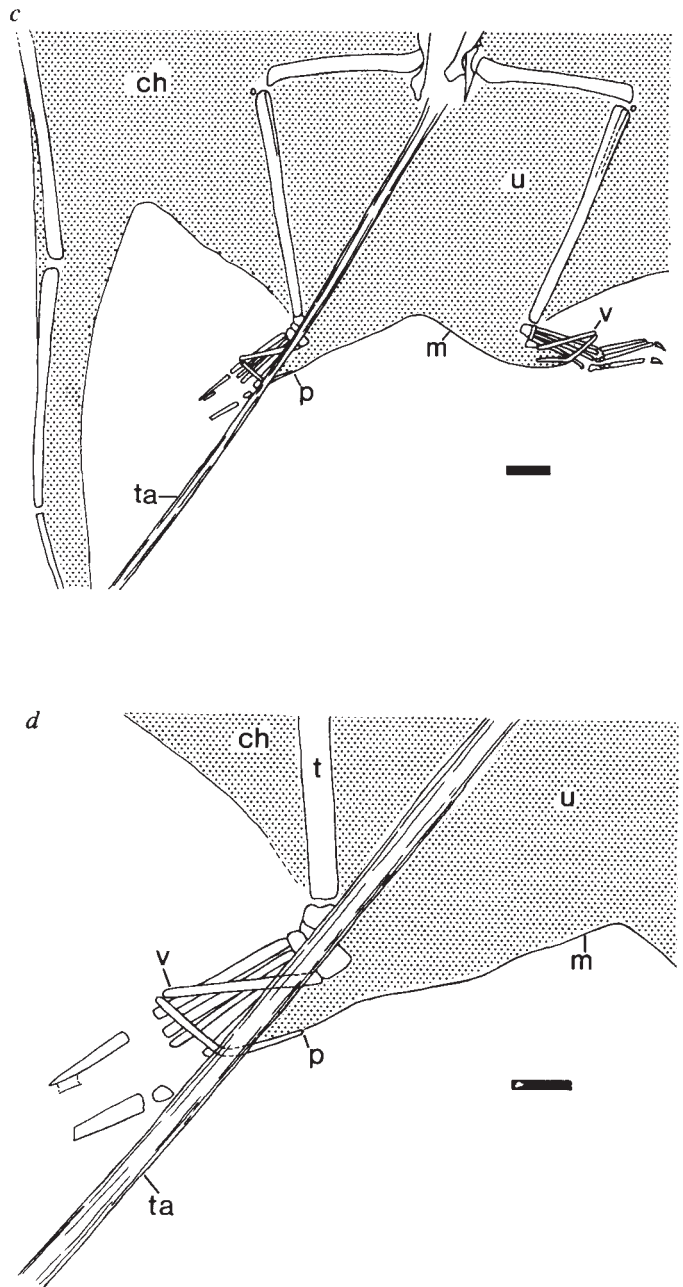
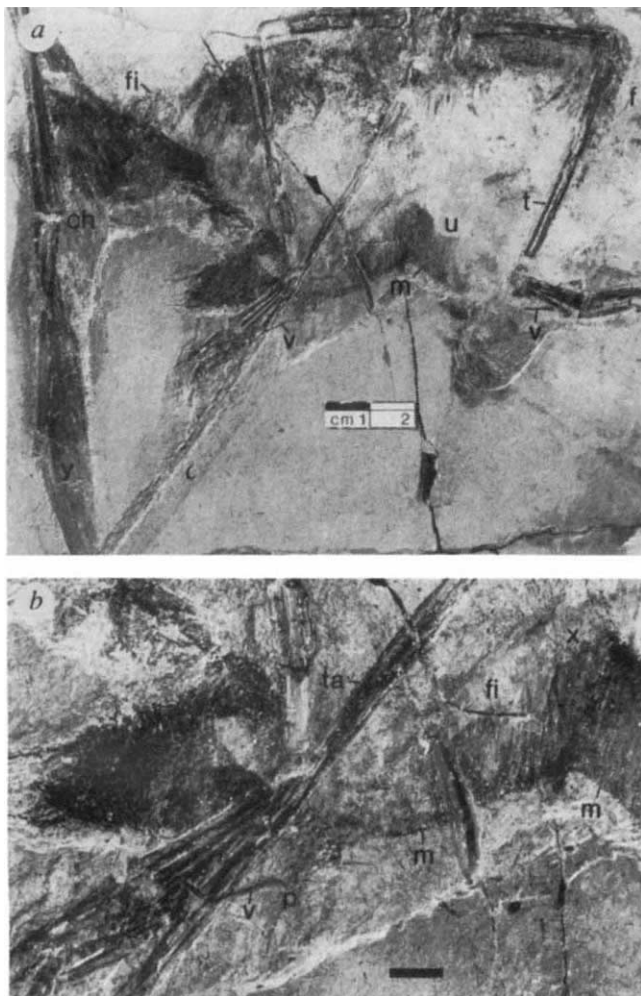


FIG. 1 *Sordes pilosus* (PIN 2585/3). a, Dorsal view of the left wing-finger, the hindlimbs and associated wing membranes. b, Details of the left foot and uropatagium. c and d, Interpretive drawings of a and b (for clarity, only wing membranes and skeletal remains are indicated). The hindlimb is preserved in 'flight' position, with the fifth metatarsal located dorsomedial to the foot, the first phalange of the fifth toe directed laterally, and the second phalange reflected medially to insert into the rear edge of the uropatagium. Areas x and y are shown in detail in Fig. 2. Abbreviations: ch, cheiropatagium; f, fold; fi, structural fibres; m, rear or free margin of uropatagium; p, point of insertion of fifth toe into uropatagium; t, tibia; ta, tail; u, uropatagium; v, fifth toe. Scale bar in b and d, 5 mm; in c, 10 mm.



proximal regions of the cheiropatagium were somewhat softer and more elastic. This model thus provides a neat explanation for the frequently observed absence of evidence of the inner parts of the wings in, for example, Solnhofen pterosaurs<sup>1,2,6</sup>: only the tough, outer parts were preserved, whereas the softer, inner regions of the wing decayed more rapidly or were not resilient enough to leave recognizable impressions.

Contrary to recent reconstructions in which they are free of the wings<sup>1-6</sup>, the hind limbs were an important component of the flight apparatus (Fig. 3). The configuration and orientation of the cheiropatagium was controlled by the forelimb, assisted by movements of the femur and crus which controlled the position, shape and tension of its relatively elastic proximal region<sup>16</sup>. The uropatagium, probably used for manoeuvring and braking,

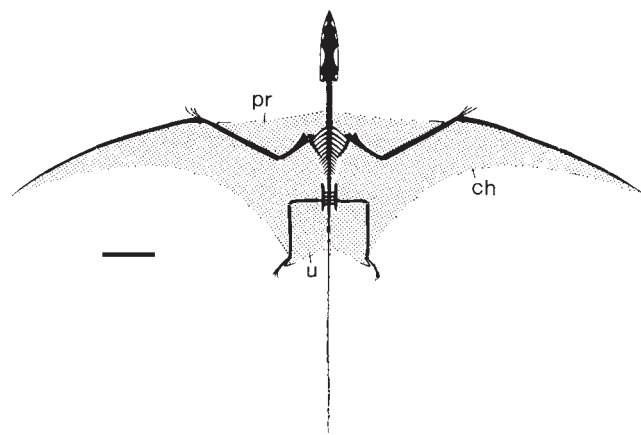


FIG. 3 Restoration of *Sordes pilosus* in dorsal view showing the relationship of the skeleton to the flight membranes. Abbreviations as for Fig. 1; pr, propatagium. Scale bar, 50 mm.

was manipulated by the fifth toe and thus functioned semi-independently of the cheiropatagium. The highly manipulable flight surface and low wing-loading<sup>22,23</sup> points to relatively slow, manoeuvrable flight in pterosaurs and is consistent with their probable modes of life as surface feeding piscivores and aerial insectivores<sup>10,24</sup>. When grounded, the attachment of patagia to the legs and feet must have severely impeded movement. This, and other evidence for a semi-erect, quadrupedal stance and gait<sup>24,27</sup>, suggests a poor terrestrial ability and a 'gravity-assisted' rather than 'ground up' origin of flight for pterosaurs, particularly as the latter requires the ability to run at relatively high speed<sup>28</sup>.

The wings of pterosaurs differ in many fundamental ways from those of modern fliers, thus, despite their popularity, models based on birds and bats have failed to provide lasting insights into the construction of the pterosaur flight apparatus. Cases of exceptional preservation such as *Sordes* and others<sup>1,2,6,9,16,21</sup>, provide a reliable basis for detailed and accurate reconstruction of pterosaur morphology without the need for recourse to arbitrary and potentially misleading analogies<sup>5</sup>. □

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- Wellnhofer, P. *Abh. Bayer. Akad. Wiss. N. F.* **141**, 1–133 (1970).
- Wellnhofer, P. *Palaeontographica* **149**, 1–30 (1975).
- Padian, K. *Paleobiology* **9**, 218–239 (1983).
- Padian, K. *Nat. Hist.* **97**, 58–65 (1988).
- Padian, K. in *Biomechanics in Evolution Sem. Ser. Soc. exp. Biol.* **36** (eds Rayner, J. M. V. & Wootton, R. J.) 146–160 (Cambridge Univ. Press, UK, 1991).
- Padian, K. & Rayner, J. M. V. *Am. J. Sci.* **293A**, 91–166 (1993).
- Pennycook, C. J. *Mem. Calif. Acad. of Sci.* **8**, 83–98 (1986).
- Pennycook, C. J. *Biol. Rev.* **63**, 209–231 (1988).
- Wellnhofer, P. *Annl. Nat. Hist. Mus. Wien* **88A**, 149–162 (1987).
- Wellnhofer, P. *The Illustrated Encyclopedia of Pterosaurs* (Salamander, London, 1991).
- Sharov, A. G. *Akad. nauk SSSR Paleont. Inst. Tr.* **130**, 104–113 (1971).
- Gekker, R. F. *Akad. nauk SSSR Paleont. Inst. Tr.* **15**, 7–85 (1948).
- Doludenko, M. P., Sakulina, G. V. & Ponomarenko, A. G. *The Geology and Late Jurassic Fauna and Flora of a Unique Locality, Aulie (Karatau Range, Southern Kazakhstan)* (Inst. Geol., Moscow, 1990).
- Riabinin, A. N. *Akad. nauk SSSR Paleont. Inst. Tr.* **15**, 86–93 (1948).
- Bakhurina, N. N. *Bull. Mos. Soc. nat. Hist. (Geol.)* **63**, 132 (1988).
- Martill, D. M. & Unwin, D. M. *Nature* **340**, 138–140 (1989).
- von Meyer, H. *Zur Fauna der Vorwelt, Vierte Abteilung* (Keller, Frankfurt-am-Main, 1859).
- Broili, F. *Sitzungsber. Bayer. Akad. Wiss., math.-naturwiss.* 23–34 (1925).
- Hazlehurst, G. A. thesis, Bristol Univ. (1991).
- Broili, F. *Sitzungsber. Bayer. Akad. Wiss., math.-naturwiss.* 139–154 (1938).
- Abel, O. *Amer. Mus. Novit.* **192**, 1–12 (1925).
- Bramwell, C. D. & Whitfield, G. R. *Phil. Trans. R. Soc.* **267**, 503–581 (1974).
- Hazlehurst, G. A. & Rayner, J. M. V. *Paleobiology* **18**, 447–463 (1992).
- Wellnhofer, P. & Vahldiek, B. W. *Palaont. Zeitschrift* **60**, 329–340 (1986).
- Unwin, D. M. *Nature* **327**, 13–14 (1987).
- Wellnhofer, P. *Hist. Biol.* **1**, 3–16 (1988).
- Wellnhofer, P. *Palaeontographica* **215**, 43–101 (1991).
- Rayner, J. M. V. in *The Beginnings of Birds* (eds Hecht, M.K., Ostrom, J. H., Viohl, G. & Wellnhofer, P.) 289–292 (Freunde des Jura-Museums Eichstätt, Willibaldsburg, 1985).

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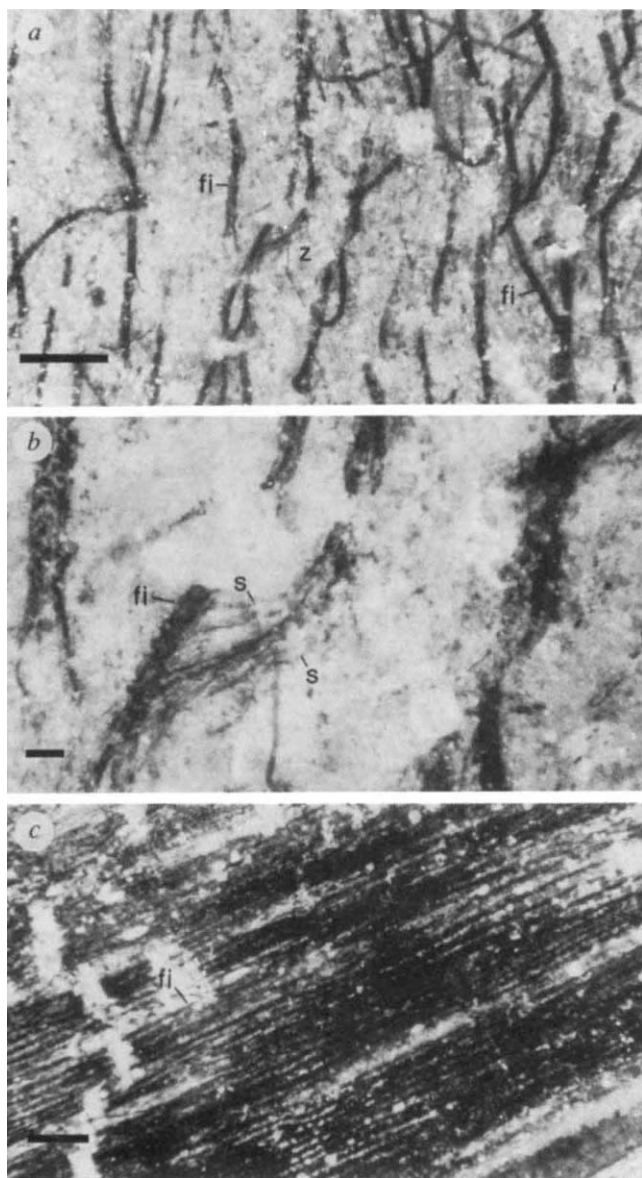


FIG. 2 Details of wing preservation in *Sordes pilosus* (PIN 2585/3). a, Structural fibres in the uropatagium, from a position corresponding to x in Fig. 1b. b, Details of the fibres from position z in a. Each fibre is a composite structure, contrary to recent descriptions of them as solid elements<sup>5,6</sup>, consisting of numerous ultrafine strands and preserved here as they became partly un unravelled. c, Structural fibres in the wing tip, from position y in Fig. 1a. Abbreviations: fi, structural fibres; s, strand. Scale bar in a and c, 1 mm; in b, 0.1 mm.