

The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathinae) and the structure of the pterosaur wing membrane

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The soft tissue preserved in the holotype (IVPP V12705) of *Jeholopterus ningchengensis* from the Daohugou Bed (Late Jurassic or Early Cretaceous) of China is described in detail. The plagiopatagium can be divided into the distal, comparatively more rigid actinopatagium and a proximal, more tensile tenopatagium. The actinopatagium extends from the wing finger to the articulation between the humerus and the forearm, and shows the presence of at least three layers containing actinofibrils. In each layer, the actinofibrils are parallel to subparallel, but this direction diverges from layer to layer. When distinct layers of actinofibrils are superimposed (owing to taphonomic compression), a reticular pattern is generated. The presence of layers with differently oriented actinofibrils is widespread in this pterosaur. A well-developed integumental covering formed by fibres (here named pycnofibres) that are thicker than the actinofibrils is present. Ungual sheaths that extend the length of the pedal and manual claws of this taxon are also observed. Although the understanding of the mechanical properties of the wing membrane is hampered by the lack of knowledge regarding the composition of the actinofibrils, the configuration observed in *Jeholopterus* might have allowed subtle changes in the membrane tension during flight, resulting in more control of flight movements and the organization of the wing membrane when the animal was at rest.

Keywords: Pterosauria; soft tissue; wing membrane; *Jeholopterus*; Daohugou Bed; China

1. INTRODUCTION

Fossil deposits containing pterosaurs with soft tissue preservation are quite rare in geological records. To date, specimens presenting the soft anatomy of this extinct group of flying reptiles were reported from Triassic strata of Lombardy and Udine in Italy (Wild 1993; Dalla Vecchia 1994), from the Lower Jurassic of Holzmaden (Broili 1939; Padian 2008) and the Upper Jurassic Solnhofen limestone (e.g. Goldfuss 1831; Frey & Martill 1998; Frey *et al.* 2003) in Germany, from the Upper Jurassic Karatau of Kazakhstan (Sharov 1971; Unwin & Bakhurina 1994) and from the Lower Cretaceous Crato (e.g. Sayão & Kellner 1998; Frey & Tischlinger 2000) and Romualdo formations (Campos *et al.* 1984; Martill & Unwin 1989; Kellner 1996) of the Araripe Basin in Brazil.

More recently, fossils preserving wing membranes and other soft tissues were also recovered from the Jehol

Group, more specifically from the Daohugou Bed (Czerkas & Ji 2002; Wang *et al.* 2002), the Yixian (Lü 2002; Wang *et al.* 2007) and Jiufotang Formations. Although the first described pterosaur from those deposits also shows nice preservation of wing membrane and skin associated with the gastralia (not mentioned in the original description; Ji & Ji 1997; Wang *et al.* 2007) and the number of new specimens increases steadily (e.g. Wang *et al.* 2005, 2008; Lü *et al.* 2006), Chinese material with soft tissue has not been reported extensively.

Despite the fact that specimens with preserved soft anatomy from other deposits have been known for quite a long time (e.g. Zittel 1882; Sharov 1971; Padian & Rayner 1993), there is considerable disagreement on their interpretation. Particularly, the nature of the patagium (the skin that forms the soft part of the wing), including the extent to which it involves the hind limbs and the presence and nature of structural fibres, is the object of extensive debate (e.g. Wellnhofer 1987; Pennycuik 1988; Padian & Rayner 1993; Bennett 2000; Peters 2002; Tischlinger & Frey 2002). There are also questions about the presence and nature of some filamentous structures covering the epidermis, the so-called 'hair-like' fibres or 'fur' (Goldfuss 1831; Sharov

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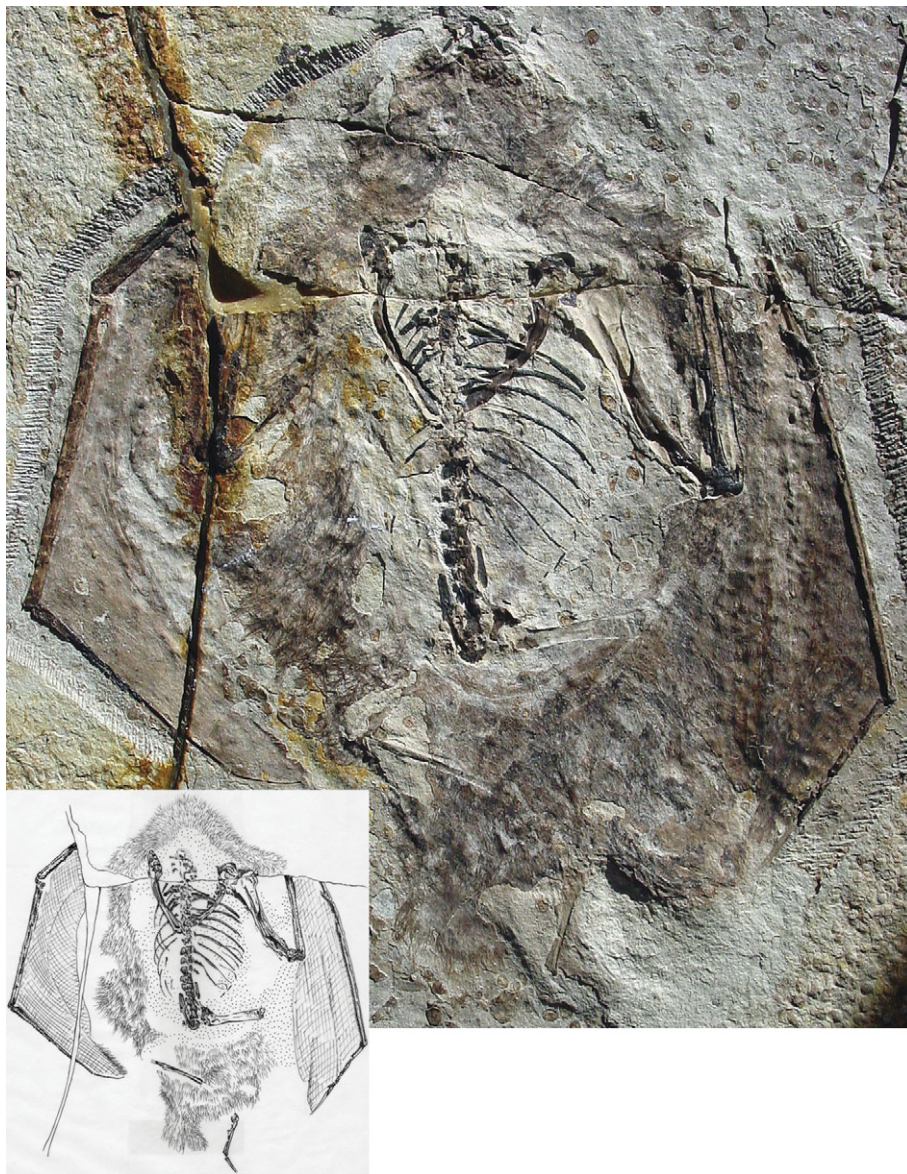


Figure 1. *Jeholopterus ningchengensis* (IVPP V12705), top slab under natural light. Sketch indicates the bones and the different soft tissue preserved. Scale bar, 50 mm.

1971; Unwin & Bakhurina 1994), which were also found in specimens from the Jehol Group and regarded as potential protofeathers (Czerkas & Ji 2002; Ji & Yuan 2002).

The most complete pterosaur specimen from China with soft tissues is the holotype (IVPP V12705) of *Jeholopterus ningchengensis*. Representing a rather large anurognathid with a wing span of 90 cm (Wang *et al.* 2002), it consists of an almost complete skeleton that was recovered from the Daohugou Bed at Ningcheng of Inner Mongolia, near Lingyuan, west Liaoning. The age of those strata is controversial, with some authors regarding them as having been formed as early as the Middle Jurassic (Chen & Zhang 2004), while others provide evidence for a younger age (Late Jurassic–Early Cretaceous; Wang *et al.* 2002; Zhang 2002; He *et al.* 2004).

The soft tissue of *J. ningchengensis* (IVPP V12705) is studied here in detail. We also include investigation under ultraviolet light following a procedure that has yielded relevant anatomical information in other pterosaur material (e.g. Tischlinger & Frey 2002). The analysis of this spectacular fossil provides new data on the hair-like filaments (here called pycnofibres) that cover most of the

animal's body and allows a rediscussion of the internal anatomy of the pterosaur wing membrane.

2. SYSTEMATIC PALAEONTOLOGY

In the original description, Wang *et al.* (2002) correctly referred *J. ningchengensis* to the Anurognathidae, a clade composed of *Anurognathus*, *Batrachognathus* and *Dendrorhynchoides*. In a phylogenetic study, Kellner (2003) established that *Batrachognathus* and *Dendrorhynchoides* were closely related, for which he created the clade Asiaticognathidae. Subsequent cladistic analyses performed by Kellner (2004a,b) and Wang *et al.* (2005) resulted in an unresolved grouping of *J. ningchengensis*, *Batrachognathus* and *Dendrorhynchoides*.

As noted by Bennett (2007), the family name Asiaticognathidae is inappropriate as it was not based on an included genus. Therefore, we propose the name Batrachognathinae, defined as all anurognathids related more closely to *Batrachognathus* than to *Anurognathus ammoni*. Presently, the Batrachognathinae is composed of *Batrachognathus volans*, *Dendrorhynchoides curvidentatus* and *J. ningchengensis*.

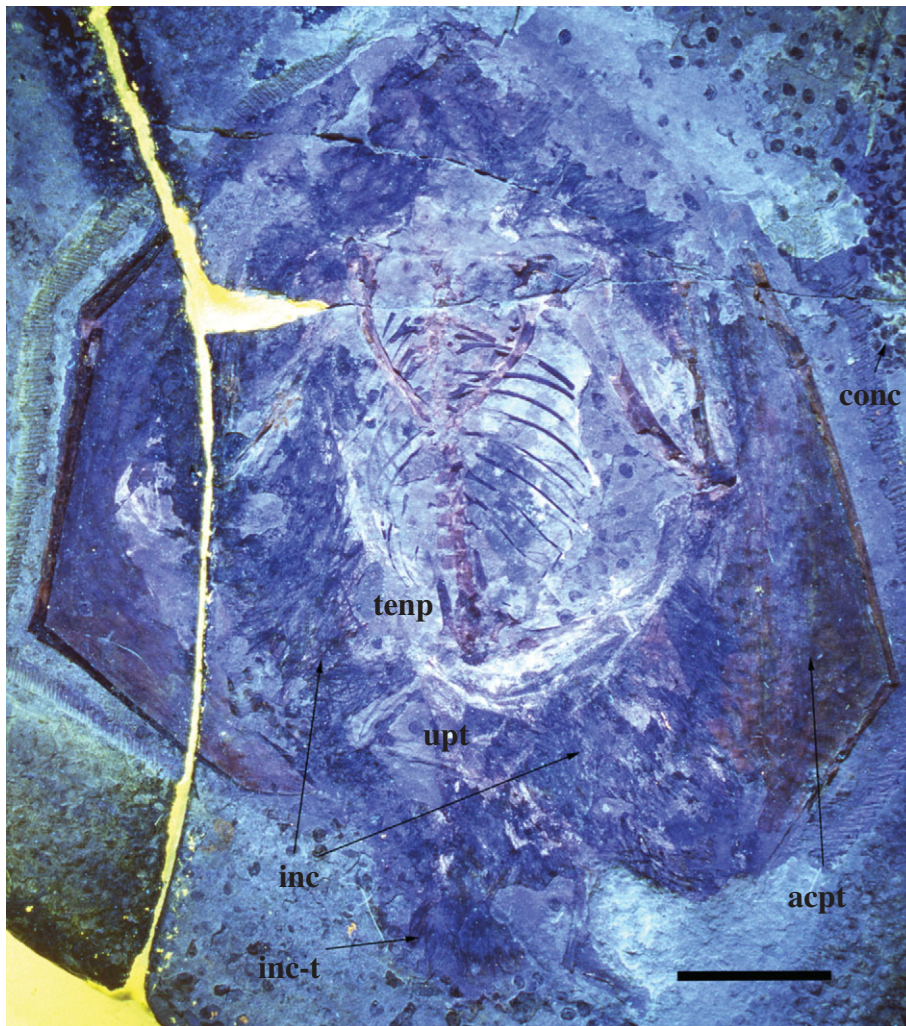


Figure 2. *Jeholopterus ningchengensis* (IVPP V12705), top slab, under ultraviolet light. The yellowish substance is resin that was employed to glue parts of the specimen. Note the whitish matter, interpreted as the epidermis (and part of the dermis; see text). Scale bar, 50 mm. acpt, actinopatagium; conc, conchostracans; inc, integumental covering; inc-t, integumental covering of the tail; temp, tenopatagium; upt, uropatagium.

3. DESCRIPTION AND COMPARISONS

(a) *General aspects*

The holotype of *J. ningchengensis* is preserved in a slab of tuffaceous shale along with several conchostracans. The rock was split and most of the skeleton remained on the bottom slab, which also represents the bottom of the former lake where the carcass came to a stop before final burial. The top slab contains most of the wing finger, both scapulae, most of the ilia and part of several dorsal vertebrae, including nearly all ribs from the left side (figure 1). Bones are dark brown, with the external surface not well preserved, particularly the pelvic region and the hind limbs. The skeleton is exposed essentially in dorsal view and, except for the tail, all bone elements are present (Wang *et al.* 2002) with negligible post-mortem disturbance. The wings are partially folded against the body but do not overlap, with each manus positioned close to the skull and the tip of the left wing finger partially overlying the left pes. The right wing finger is dislocated from the wing metacarpus towards the skull, with the fourth wing finger phalanx positioned close to the knee joint.

Soft tissues are observed all around the skeleton (figures 1–4). The colour varies from tones of brown to

light cream and beige. Parts of the soft tissue show distinctive structures, indicating that they are of different nature.

In comparison with other pterosaur specimens with soft tissue, the material of *J. ningchengensis* is among the most complete ever reported, associated with almost the entire skeleton of the animal. In most other deposits, only traces or limited portions of soft tissue are found, including the specimens of the Crato and Romualdo Formations (e.g. Campos *et al.* 1984; Sayão & Kellner 1998; Frey & Tischlinger 2000). The same seems to be true of the pterosaurs of the Solnhofen limestone, although one exceptional specimen also shows extensive soft tissue preservation (Tischlinger & Frey 2002).

Most soft tissues of this *Jeholopterus* specimen appear to be carbonized but some areas, particularly around the body, might have been phosphatized as suggested by the whitish colour, similar to the exceptional three-dimensionally preserved material from the Romualdo Formation (e.g. Kellner & Campos 1999).

(b) *Propatagium*

The propatagium is not well preserved. On the left side, the distal segment is partially covered by matrix and the

visible remains are mainly associated with the radius, the ulna and the distal part of the humerus. Traces of elongated fibres are visible, running subparallel to the main axis of the ulna and radius. On the right side, the propatagium is preserved along the pteroid and the proximal part of the humerus, also showing faint structural fibres. In both sides, the pteroid is dislocated from its anatomical position (e.g. with the proximal carpal series) and is preserved associated with the radius and ulna, positioned at a right angle with those bones. The metacarpal region on the left side is covered by matrix, but on the right side it was exposed and there is no extension of the propatagium distal to the carpal region; if originally present, it was removed during preparation.

Little information regarding the propatagium has been published so far (e.g. Frey *et al.* 2003). Traces of the propatagium are found in the ‘Zittel wing’ (referred to *Rhamphorhynchus muensteri*), but most of it has been removed during preparation (Padian & Rayner 1993). Another exceptionally preserved *R. muensteri* (informally known as the ‘dark wing’) also lacks detailed evidence of the internal anatomy of the propatagium (Tischlinger & Frey 2002; Frey *et al.* 2003). In one *Pterodactylus* specimen, Wellnhofer (1987) mentioned the presence of faint impressions of structural fibres that he regarded as similar to the actinofibrils of the plagiopatagium.

(c) *Plagiopatagium*

The plagiopatagium is extremely well preserved along all wing elements, and there is no overlap of the left and right sides. Owing to the splitting of the rock, this portion of the wing membrane was divided, exposing mostly the internal part. The left wing also exposes the external surfaces of this portion of the wing membrane.

Although no distinctive trailing edge is discernible, the wing membrane extends along the body and is connected to the hind limbs, reaching the ankle (Wang *et al.* 2002). While the distal portion of the plagiopatagium shows several layers of closely packed fibres (actinofibrils), the more proximal part lacks these structures. This confirms the observations of Schaller (1985), who recognized two distinct portions of the plagiopatagium, the actinopatagium and the tenopatagium, distinguished by the presence and absence of actinofibrils, respectively.

Three distinct types of fibres were identified, here designated as fibres A, B and C for descriptive purposes. Type C fibres are regarded as integumental covering and are described in a separate section (discussed subsequently). Type A fibres form the majority of the actinopatagium and are identified as the actinofibrils commonly observed in pterosaur wing membrane (Wellnhofer 1987; Padian & Rayner 1993; Kellner 1996). The thickness of individual actinofibrils varies, averaging around 0.1 mm. They are closely packed and lie parallel to subparallel to the wing finger. The distance between adjacent fibres can vary, resulting in 4–7 fibres mm^{-1} . Close to the distal edge of the plagiopatagium, fibres tend to be comparatively thinner (greater than 0.1 mm), with up to 9 fibres mm^{-1} . Individual fibres are difficult to trace, with lengths varying between 4 and 8 mm. In many cases, one fibre ends between two adjacent fibres. This particular construction was also observed in *Rhamphorhynchus* (Padian & Rayner 1993, p. 126), but in *Jeholopterus*,

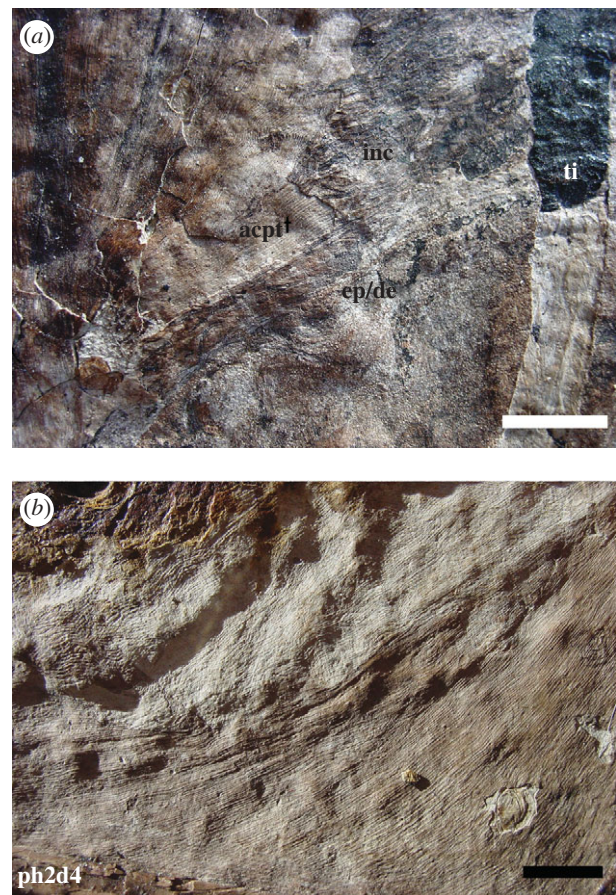


Figure 3. Details of the soft tissue of *J. ningchengensis* (IVPP V12705). (a) Region close to the right tibia (bottom slab). Scale bar, 10 mm. (b) Actinopatagium close to the second and third wing finger phalanges of the right wing. Scale bar, 1 mm. acpt, actinopatagium; ep/de, epidermis/dermis; inc, integumental covering; ph2d4, second phalanx of the wing finger; ti, tibia.

this intercalation of fibres is more common. In some areas, layers of fibres converge (figure 4a).

Among the new features observed in IVPP V12705 is the presence of up to three (and possible more) distinct layers of actinofibrils that run in different directions (figures 3a and 4a). In several places, a reticular pattern is formed owing to taphonomic compression of distinct layers with actinofibrils. This reticular pattern is widespread in this specimen, indicating that the layer with actinofibrils oriented in different directions is a common feature in the actinopatagium of this pterosaur (figure 4b). Close to the wing finger phalanges, at least two layers of actinofibrils can be identified, with the dorsal one showing the fibres running subparallel to the wing elements, which cover a second layer with fibres running towards the wing finger phalanges. The fibres of the dorsal layer tend to be thinner (0.05–0.1 mm) and more spaced (figure 3b). Close to the body and on the posterior part of the actinopatagium, the actinofibrils are bent, showing some flexibility (figure 3b).

Type B fibres are much rarer. They are thicker than the regular actinofibrils (0.2–0.3 mm) and much longer (figure 4a). In some parts, type B fibres are covered by individual actinofibrils. It is difficult to interpret them, but they could potentially be blood vessels that irrigate the wing membrane (as seen in *Rhamphorhynchus*; Frey *et al.* 2003) or a more robust actinofibril.

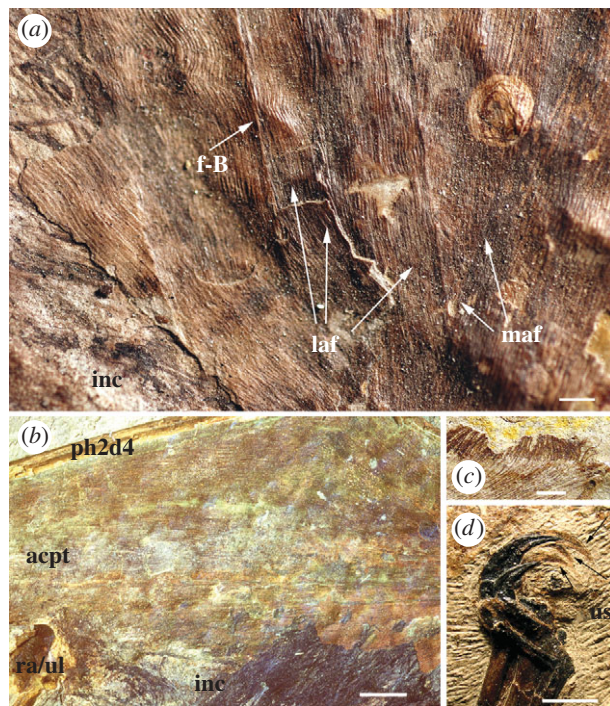


Figure 4. Soft tissue of *J. ningchengensis* (IVPP V12705). (a) Details of the actinopatagium with different layers indicated by white arrows (top slab). (b) Actinopatagium under ultraviolet light showing the difference between the actinofibrils and the integumental covering (dark colour). (c) Tip of the wing membrane associated with the fourth phalanx of the right wing finger. (d) Ungual sheaths of the right manual digits indicated by black arrows. Scale bars: (a–c) 1 mm; (d) 10 mm. acpt, actinopatagium; f-B, fibres type B; inc, integumental covering; laf, different layers of actinofibrils; maf, merging actinofibrils; ph2d4, second phalanx of the wing finger; ra/ul, radius and ulna; us, unguis sheaths.

The reticular pattern of several areas in the *Jeholopterus* patagium was also reported in a pterodactyloid from the Crato Formation (Sayão & Kellner 1998), where it was regarded as originated owing to folding of the wing membrane. However, in the light of the present specimen (IVPP V12705), this pattern is reinterpreted and indicates the presence of distinct layers of actinofibrils that were compressed dorsoventrally, owing to taphonomy. Several authors have described the actinofibrils occurring in one layer (e.g. Wellnhofer 1987; Padian & Rayner 1993; Frey *et al.* 2003), but in *Jeholopterus* (and the Crato specimen) there are several layers with those structural fibres.

Close to the body, the presence of actinofibrils reduces gradually, showing the beginning of the tenopatagium. Although the exact limits between the actinopatagium and tenopatagium are difficult to trace, based on preserved actinofibrils, the actinopatagium was developed proximally until close to the articulation of the humerus and forearm.

(d) Uropatagium

The uropatagium is not well preserved. Most of this membrane is encased in the bottom slab (plate I, fig. 2 in Wang *et al.* 2002), but traces can also be found in the top slab (figures 1 and 2). The shape of the uropatagium cannot be determined owing to the lack of a distinct posterior edge and the medially displaced feet. Two sets of fibres are observed: one running parallel to the

longitudinal axis of the body and the second running perpendicular to the tibiae. This pattern is not as well developed as in the actinopatagium but, based on the thickness of the fibres, they are of the same nature as the actinofibrils. Integumental covering is also found.

An uropatagium was observed in *Sordes pilosus* with a well-preserved posterior edge (Sharov 1971; Unwin & Bakhurina 1994). In this species, fibres are present, running parallel to the main axis of the body. Patches of the uropatagium were also reported in *Rhamphorhynchus* (Frey *et al.* 2003), although it is not clear if it bears any structural fibres.

(e) Epidermis/dermis

Amorphous matter with a distinctive rugose surface is observed mainly close to the body (figure 3a), which differs from the bones, the soft tissues of the actinopatagium and the texture of the sedimentary rock. This material is not an impression of some sort and is commonly associated with type C fibres (regarded as integumental structures) since all of it lies in the tenopatagium and largely traces the edge of the torso and the ribs. Under ultraviolet light, it shines peculiarly white and can easily be distinguished from the other tissues (figure 1). Based on the present evidence, this material is interpreted as patches of the epidermis (possibly with part of the dermis as well). No wrinkles of the stratum corneum—observed in an exceptional specimen from the Romualdo Formation (Kellner 1996)—could be identified, possibly as a result of decay. Although no chemical analysis of this soft tissue was conducted, phosphatization such as has occurred in other vertebrate soft tissue materials (e.g. Kellner & Campos 1999) could potentially have contributed to this preservation in the Chinese specimen.

(f) Integumental covering (pynofibres)

On the tenopatagium close to the body and on the tail, a third type of fibre with somewhat diffuse edges is observed (figures 3a and 4a). Type C fibres can be easily separated from other fibres by their dark-brown colour and their general lack of organization. They are distributed along the body, the tail and the tip of the actinopatagium close to the fourth wing finger phalanx (figures 1, 2 and 4c). Sometimes clustering together, they are not found covering the external portion of the plagiopatagium and are apparently rare on the actinopatagium.

Generally thicker than the actinofibrils (figure 4a), type C fibres have an average thickness ranging between 0.2 and 0.5 mm. In several places, it is clear that they are formed by smaller fibrils, the nature of which is unknown. The sediment between type C fibres tends to be light brown in colour, making the distinction of individual fibres more difficult. Several cross each other but lack the reticular pattern formed by the multi-layered superposition of the actinofibrils. In several areas, type C fibres are preserved associated with an amorphous whitish matter that has been interpreted as patches of the epidermis (and dermis, described earlier). Although not parallel to each other and lacking the organization of the actinofibrils, fibres C in most parts are generally displaced away from the skeleton.

As Wang *et al.* (2002) pointed out, these fibres are best interpreted as structures covering the body, commonly referred to as 'hair' or hair-like structures (e.g. Sharov 1971; Bakhurina & Unwin 1995). This pterosaur hair, which is not homologous to the mammalian hair (a protein filament that originates deep in the dermis and grows through the epidermis), is here called pycnofibre (from the Greek word *pyknos*, meaning dense, bushy). The pycnofibres are further formed by smaller fibrils of unknown nature. They were possibly mostly composed of keratin-like scales, feathers and mammalian hair.

(g) *Ungual sheaths*

The manual and pedal unguals of *Jeholopterus* are long and curved, with a broad and high proximal part and a very thin and pointed distal end. More interestingly, they are covered by a brownish matter, here interpreted as keratinous unguual sheaths (figure 4d). On the right manus only two unguals are observed, but the unguual sheaths indicate the presence of a third unguual that must be still embedded in the sediment. Overall, the unguual sheaths in *Jeholopterus* indicate that the manual and pedal claws in this taxon extended the length of the bony part by almost 40 and 20 per cent, respectively.

Ungual sheaths have rarely been reported in pterosaurs. In *Pterodactylus* and a pterodactylid from the Crato Formation, the pedal unguual sheaths are almost double the size of the bone (e.g. Frey *et al.* 2003), but in *Jeholopterus*, they are comparatively shorter. No manual unguual sheaths are reported in the literature so far. Wang *et al.* (2002) also noted that the feet of *Jeholopterus* are webbed, which has also been observed in other pterosaurs (e.g. Frey *et al.* 2003).

4. DISCUSSION

The wing membrane of *Jeholopterus* agrees with the current idea that the plagiopatagium is composed of a distal stiffer part and a more tensile and more flexible (perhaps also elastic) proximal part. Those distinct regions were called actinopatagium and tenopatagium, respectively (Schaller 1985). Apparently, the propatagium and the uropatagium are similar to the actinopatagium, although being perhaps more tensile owing to the smaller number of actinofibrils.

Shortly after the description of *J. ningchengensis* by Wang *et al.* (2002), Peters (2002) argued that the wing membrane in the Chinese taxon did not reach the ankle but extended only to the elbow. However, despite the fact that no trailing edge of the posterior portion of the plagiopatagium is clearly discernible, an extensive portion of soft tissue that is attributable to the wing membrane is closely associated with the hind limbs, particularly with the tibiae (figure 3a). Apparently, Peters (2002), who based his studies on photographs, has only identified the limits of the actinopatagium, which indeed terminate at the articulation of the humerus with radius and ulna, but the tenopatagium extends up to the ankle.

The presence of two distinct parts of the plagiopatagium was also observed in *Sordes*, *Rhamphorhynchus* and *Pterodactylus* (Unwin & Bakhurina 1994; Bennett 2000; Tischlinger & Frey 2002). According to Bennett (2000), the actinopatagium reached the midpoint of the ulna in *Rhamphorhynchus* (Zittel wing) and the carpus in

Pterodactylus, further suggesting that there is some variation in the extent of the actinopatagium within pterosaurs. In *Jeholopterus*, the actinopatagium is comparatively more extended proximally, closer to the articulation between humerus and ulna, which appears to be also the case with *Sordes*. Although the sample of pterosaur species with preserved plagiopatagium is still very limited, it seems that the actinopatagium was more extended in basal taxa.

There are presently four competing models for the internal structure of the pterosaur wing membrane. Wellnhofer (1987) suggested that the actinofibrils were structural fibres embedded in the wing membrane. Pennycuick (1988) disagreed with this interpretation and regarded the 'fibres' as wrinkles caused by the inner elastic fibres contracting after the animal's death. In a review of pterosaur wing membrane, Padian & Rayner (1993) argued for the presence of structural fibres on the surface of the ventral part of the wing membrane, closely associated with the epidermis. Lastly, Tischlinger & Frey (2002) and Frey *et al.* (2003), based on a *Rhamphorhynchus* specimen from Solnhofen and an exceptionally well-preserved material from the Romualdo Formation (DGM 1475-R) of Brazil (Martill & Unwin 1989; Kellner 1996), interpreted the pterosaur plagiopatagium as consisting of five layers from dorsal to ventral: a thin and 'hairless' epidermis, a spongy subdermis, a layer of actinofibrils, a layer of dermal muscles and a vascular layer. Regarding the last model, it should be noted that Kellner (1996) regarded the soft tissue present in the specimen of the Romualdo Formation as closely associated with the body.

The specimen of *J. ningchengensis* adds new information to this discussion. There seems little doubt that the actinofibrils are, in fact, structural fibres, contradicting Pennycuick's (1988) interpretation as superficial wrinkles introduced by elastic fibres. Actinofibrils are internal structures, favouring Wellnhofer's (1987) assumption, and no evidence was found that they are positioned on the ventral part of the plagiopatagium and therefore directly associated with the epidermis as supposed by Padian & Rayner (1993).

Although the model proposed by Tischlinger & Frey (2002) uses information of a controversial pterosaur specimen from the Romualdo Member (see Kellner 1996 for a detailed discussion), the idea that the pterosaur wing membrane is composed of several layers is somewhat expected and has been defended before (e.g. Padian & Rayner 1993; Bennett 2000). The material of *J. ningchengensis* agrees with this general concept, but differs from all other models by clearly showing that there is not one but several (at least three) layers of actinofibrils. No evidence of a separate layer of blood vessels was found, but it is likely that one existed. There is evidence in the Chinese specimen of the epidermis (+dermis) that covers the layers of plagiopatagium, for the entire tenopatagium and also parts of the actinopatagium (figure 3a). Since the epidermis covering the most distal part of the actinopatagium is not well preserved, we hypothesize that the external layer of the skin of the plagiopatagium became thinner distally.

According to Unwin & Bakhurina (1993) and Frey *et al.* (2003), actinofibrils become thinner towards the body and might have had a reduced fossilization potential.

In the *Jeholopterus* specimen, there is a well-marked distinction between the region of the actinopatagium and the tenopatagium, although the exact limits between those areas cannot be established with great precision. Therefore, while some merging between the distinct parts of the plagiopatagium must have occurred, there is no reason to suppose that the tenopatagium close to the body contained fibres or that they would diminish in thickness.

It should be noted that the exact composition of the actinofibrils is still an open question, hindering the establishment of the mechanical properties of the wing membrane. Padian & Rayner (1993) argue that those structural fibres might have been keratinous, homologous of scales and feathers. However, being internal structures not closely associated with the epidermis, this composition seems unlikely. Bats have a complex patagium with collagen, striated muscles and elastic fibres (Gupta 1967; Holbrook & Odland 1978), although the plagiopatagium of *Jeholopterus* differs from those of bats owing to the presence of several layers of actinofibrils. The variation of space between adjacent actinofibrils in *Jeholopterus*, also reported in *Rhamphorhynchus* (Padian & Rayner 1993), suggests that those fibres were connected by some elastic tissue that enabled them to spread apart or join whenever necessary, making the actinopatagium more flexible (perhaps somewhat elastic; figure 3*b*). Furthermore, at least in *Jeholopterus*, actinofibrils commonly end between two others, a configuration that could potentially shorten or expand and therefore provide more flexibility to the wing membrane. Although those structural fibres are displaced parallel (or subparallel) in the same layer, the actinofibres of distinct layers differ in their directions.

In any case, the holotype of *J. ningchengensis* indicates that there was greater flexibility (perhaps also elasticity) in the wing membrane than previously thought. Therefore, it is conceivable that the particular arrangement of multi-layers containing actinofibrils would allow subtle changes in the membrane tension during flight, resulting in a more accurate control of flight movements. Furthermore, this arrangement could have helped organize the wing membrane when the animal was on the ground. The suggestion of a chordwise-spreading function (Bennett 2000) or as a load-bearing and cambering device of the actinofibrils (Padian & Rayner 1993) is not contradicted by the present model.

Some dinosaur specimens from the Jehol group also display soft tissues that have been regarded as protofeathers (e.g. Xu *et al.* 2001; Zheng *et al.* 2009). Recently, some authors have argued against this interpretation and advocated that the 'protofeathers' are the result of decayed collagen fibres embedded inside the dinosaur skin (e.g. Lingham-Soliar *et al.* 2007). Although the discussion of the dinosaurian protofeather issue is beyond the scope of this paper, the holotype of *J. ningchengensis* clearly shows fibres that are best interpreted as integumental covering.

Two other Chinese specimens were reported with integumental covering, coming from the same stratum (the Daohugou Bed) as *Jeholopterus*. So far we have not had the opportunity to examine this material. The first one is a small unnamed anurognathid with extensive preservation of soft tissue, including fibres that have been interpreted as protofeathers (Ji & Yuan 2002).

The published pictures show that the soft tissue interpreted as protofeathers is of the same nature as the pycnofibres of *Jeholopterus*. There is no indication of branching structures that are expected for feather precursors. Although from the phylogenetic position most authors tend to agree that pterosaurs are closely related to dinosaurs (e.g. Sereno 1991; Padian & Rayner 1993; Kellner 2004*a*), regarding those structures as protofeathers implies that dinosaurs and closely related taxa must originally have had similar integument covering that in more derived theropod taxa (including birds) eventually developed into feathers. There is presently no such evidence, despite much well-preserved dinosaur material (e.g. Zheng *et al.* 2009). If other phylogenetic positions regarding pterosaurs as more primitive within archosauriforms (e.g. Bennett 1996) or even closely related to protosaurs (Peters 2000; but see Hone & Benton 2007) are accepted, the case regarding pycnofibres as protofeathers is even less appealing.

In the second pterosaur, *Pterorhynchus wellnhoferi*, Czerkas & Ji (2002) recognized actinofibrils, but also some 'pinnate fibres' that, according to them, are densely aligned, forming distinct tufts in a diamond- and V-shaped pattern, covering the plagiopatagium. Those authors further mention the presence of occasional rounded structures interpreted as calami. The published pictures of this specimen reveal the existence of several kinds of soft tissue. Among those are patches of a white matter (figs 24–27 in Czerkas & Ji 2002), here interpreted as the remains of the epidermis/dermis. We could also observe several distinct layers of actinofibrils, which, in some areas, present a reticular pattern similar to *Jeholopterus* (figure 3*b*). Based on the published pictures of *Pterorhynchus*, we were unable to recognize the distinct tufts forming any pattern. The rounded structures interpreted as calamus, the basal structure of a true feather, are intriguing. However, they are not hollow and have distinct convex outlines, contradicting their interpretation as true feather (or feather-like) calami and might not be directly related to the soft tissue.

Another very important specimen containing pycnofibres is *S. pilosus*, from the Upper Jurassic Karatau of Kazakhstan. In addition to the wing membrane, Sharov (1971) interpreted some fibres as representing hair-like structures. These were subsequently questioned by Unwin & Bakhurina (1994), who regarded them as part of decomposed actinofibrils. Later, Bakhurina & Unwin (1995) briefly mentioned the occasional existence of fibre-like structures in the holotype of *Sordes*, but stated that they are not preserved enough for an accurate identification. Nonetheless, Bakhurina & Unwin (1995) mentioned the existence of hair (i.e. pycnofibres) in the paratype of *S. pilosus*, mainly confined to the region of the soft tissue associated with the posterior margin of the skull. Examination of the specimen and the published pictures (Unwin & Bakhurina 1994) reveals the presence of fibres around the body of the same nature as the pycnofibres observed in *Jeholopterus*, also concentrated in the tenopatagium. In the holotype of *Sordes*, pycnofibres are distinguishable around the femur and tibia, and differ from the actinofibrils present in the actinopatagium. Therefore, we conclude that Sharov (1971) was at least partially correct when he identified those fibres as integumental covering.

5. CONCLUSIONS

The soft tissue preserved in the holotype of *J. ningchengensis* indicates that the wing membrane is attached to the body until reaching the ankle. It also concurs with the general notion that the plagiopatagium can be divided into two distinct functional parts: the more distal actinopatagium that contains extensive actinofibrils and a softer, perhaps more flexible, proximal tenopatagium. The Chinese specimen further shows that the plagiopatagium of this pterosaur is formed by an external epidermis, followed by several layers (at least three) with closely packed actinofibrils. Part of the plagiopatagium, particularly the region closer to the body (the tenopatagium), was extensively covered by elongated and thick fibres here called pycnofibres. Individual pycnofibres are formed by fibrils of a different diameter, the nature of which is unknown. Regarding other pterosaur specimens, at least *S. pilosus* has a similar extensive integumental covering as noted in the original description (Sharov 1971).

The presence of a reticular pattern resulting from the dorsoventral compression of distinct layers of actinofibrils in phylogenetically distinct taxa such as *Jeholopterus*, which occupies a basal position within pterosaurs (Kellner 2004b), the non-pterodactyloid *Pterorhynchus* and a possible tapejarid pterodactyloid from the Crato Formation (Sayão & Kellner 1998), suggests that the presence of multi-layered actinofibrils in the wing membrane was widespread among pterosaurs.

In order to establish the mechanical properties of the wing membrane, it is paramount to understand the composition of the actinofibrils. It is desirable that future studies focus on a way to differentiate collagen and muscle fibres that could potentially be of the nature of the actinofibrils. In any case, based on *Jeholopterus*, the wing membrane of pterosaurs appears to be more flexible than previously thought (e.g. Wellnhofer 1987; Padian & Rayner 1993) and the discovery of layers containing actinofibrils with changing directions suggests that this might have influenced both flight and the arrangement of the wing membrane in the resting position.

Pycnofibres were not exclusive to *Jeholopterus* but were also present in the primitive non-pterodactyloid *S. pilosus*. Although pycnofibres have been found in other, more derived pterosaurs (Goldfuss 1831; Tischlinger & Frey 2002), none displays the extensive integumental covering other than *Jeholopterus* and *Sordes*. The fact that one exceptionally preserved specimen showing the epidermis covering the body of a pterosaur from the Romualdo Member lacks any evidence of pycnofibres (Martill & Unwin 1989; Kellner 1996) suggests that there was a great variation in integumental covering among pterosaurs. It is also possible that pycnofibres were loosely attached to the body and could be readily lost after death, especially if the carcass was floating in the water for a while.

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