Historical Biology
Vol. 22, No. 4, December 2010, 394–402

Possible link connecting reptilian scales with avian feathers from the early Late Jurassic of Kazakstan

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(*Received 15 July 2009; final version received 17 February 2010*)

Organic tissue of a recently found second specimen of feather-like *Praeornis* from the Karabastau Formation of the Great Karatau Range in southern Kazakstan, has a stable carbon isotope composition indicative of its animal affinity. Three-dimensional preservation of its robust carbonised shaft indicates original high contents of sclerotic organic matter, which makes the originally proposed interpretation of *Praeornis* as a keratinous integumental structure likely. The new specimen is similar to the holotype of *Praeornis* in the presence of three 'vanes' on a massive shaft not decreasing in width up to near its tip. Unlike it, the vanes are not subdivided into barbs and the pennate structure is expressed only in the distribution of organic-matter-rich rays. Similar continuous blades border the 'barbs' in the holotype, but the organic matter was removed from them by weathering. It is proposed that the three-vaned structure is a remnant of the ancestral location of scales along the dorsum and their original function in sexual display, similar to that proposed for the Late Triassic probable megalancosaurid *Longisquama*. Perhaps subsequent rotation around the shaft, in the course of evolution from an ancestral status similar to *Praeornis* towards the present aerodynamic and protective function of feathers, resulted in the tubular appearance of their buds.

Keywords: birds; evolution; Karatau; lake; Mesozoic

Introduction

In evolutionary terms, feathers make a bird. Their origin is a matter of a deep controversy and such is also the question of the birds' ancestry. Although mechanisms controlling development of the feather bud in present-day birds are relatively well known (Alibardi 2006, 2007a, 2007b; Toni et al. 2007), this does not help much in resolving the problem because nothing very similar is known in reptiles.

Some workers are indifferent regarding scales or tubercles as the ancestral reptilian epidermal structure (Brush 1996) or even propose that the dermal papilla originated by reduction of the archosaurian scale and its subsequent invagination together with the collar epidermis, from which the feather originated (Alibardi 2004). Others declare that the homology of feathers and scales is weakly supported, alternatives to the theropod origin of feathers are rejected, and the aerodynamic theory of feather origins is claimed falsified (Prum and Brush 2002; Prum 2005). It is generally believed that feathers originated as a cylindrical epidermal invagination (feather follicle) around the base of a dermal papilla. The first feather was proposed to be an undifferentiated cylinder, then a tuft of unbranched barbs developed, and with the origin of the rachis and barbules, the bipennate feather evolved, according to this view (Prum 1999).

Apart from the developmental studies, a support of such strong views was looked for in discoveries of 'feathered dinosaurs' in the Early Cretaceous Jehol fauna in China (Zhang et al. 2006). However, some scepticism surrounds these findings, both regarding whether they are keratinous or collagenous structures (e.g. Lingham-Soliar 2003; Lingham-Soliar et al. 2007) and whether the Chinese truly feathered 'dinosaurs' are actually not secondarily flightless birds (Feduccia et al. 2007).

To test all those contradictory theories, a fossil material preceding stratigraphically the oldest unquestionable bird *Anchiornis* from the Late Jurassic (Oxfordian?) of China (Hu et al. 2009) is desirable. Perhaps the Chinese Mid Jurassic skeletons of *Epidendrosaurus* (Zhang et al. 2002) and *Epidexipteryx* (Zhang et al. 2008) from the Daohugou Formation of Inner Mongolia, and probably *Scansoriopteryx* (Czerkas and Yuan 2002) represent such forms. There is also a putative fossil feather of age older than the Solnhofen lithographic limestone and at least as old as the Tiaojishan Formation that yielded *Anchiornis*, namely *Praeornis* from the Karabastau Formation of the Karatau Range, Kazakstan (Rautian 1978). Despite its feather-like organisation, the avian nature of *Praeornis* was questioned by Bock (1985) and most authors have supported this opinion until recently (e.g. Kellner 2002).

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ISSN 0891-2963 print/ISSN 1029-2381 online

DOI: 10.1080/08912961003710616
http://www.informaworld.com

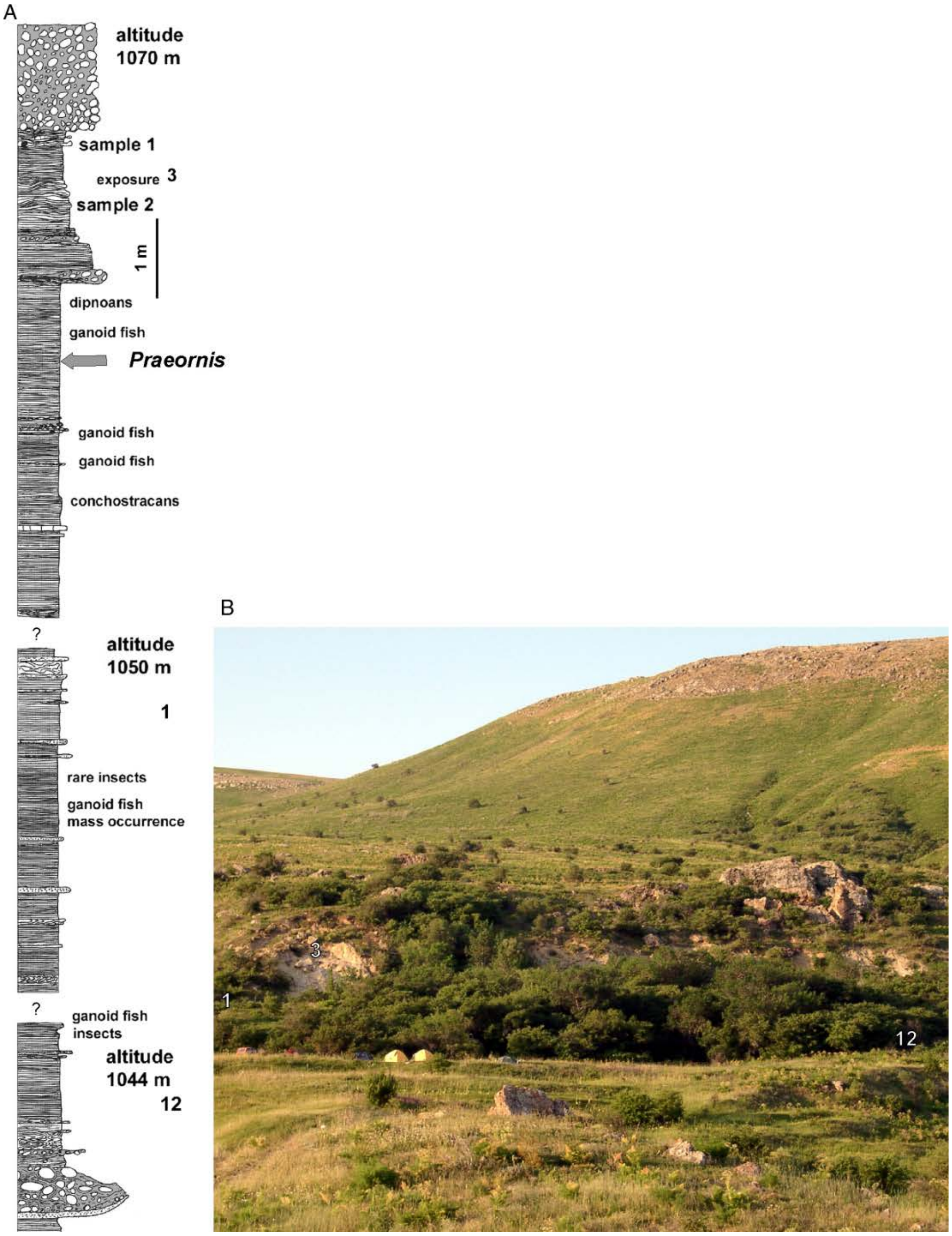

Figure 1. Composite rock column (A) of the Karabastau Formation at Aulie, Great Karatau, Kazakstan, assembled from sections at exposures 1, 3 and 12 (B) of Doludenko et al. (1990). Indicated is location of the proto-feather finding and some other fossils.

A second probable *Praeornis* 'proto-feather' was found by us in 2006. Below, we describe this new specimen and interpret it as a support to the idea of deriving feathers from scales similar to those known in the Late Triassic prolacertid *Longisquama*.

Material and geological setting

The Karatau Range is a northwestern spur of the Tian Shan Mountains in southern Kazakstan. Jurassic lacustrine deposits crop out in the part of the range referred to as the Great Karatau. They were discovered by Russian geologists in 1921 and during a few following years the list of fossil localities expanded, including the best locality now called Aulie, above the village Kasharata (formerly Mikhailovka) (Hecker 1948), coordinates 42° 53′ 50″N 70° 0′ 6″ E. In 1924 the area was declared protected as a paleontological reserve (Galicky et al. 1968). The locality is famous owing to the pterosaur *Sordes*, with preserved integumental fibres or 'fur' (Sharov 1971; Unwin and Bakhurina 1994),

The outcrop of the Karabastau Formation covers the hill slope up to an altitude of 1070 m and its exposures are scattered over the landslide area (Figure 1), down to an altitude of 1044 m (exposure 12). The bedding is mostly horizontal. Our excavations were concentrated in exposures 1 and 3 of Doludenko et al. (1990).

The most characteristic fossiliferous rock of the Karabastau Formation exposed at Aulie is a laminated claystone with less than one-millimetre thick laminae (Figure 2(E)). The dark part of each lamina is believed to represent a wet season sedimentation and increase of primary productivity in the lake, whereas its light dolomitic part presumably corresponds to a dry season (Filippova 1948). Based on this reasoning, it is estimated that the Karatau Jurassic lake existed for more than 150 thousand years (Doludenko et al. 1990). At least 10 m of laminated claystone is exposed on the hill slope but it is difficult to match particular exposures because of the landslides (Doludenko et al. 1990, fig. 5).

Near the top of the section, the lamination becomes wavy and probable microbial limestone intercalations appear, which suggests shallowing of the lake (Figure 2). The fine clastic and carbonate sedimentation ended with deposition of a thick-bedded conglomerate composed mostly of black carboniferous limestone pebbles. Conchostracans occurring in a great number in the topmost part of the section at Aulie were used as the conclusive evidence of freshwater conditions (Galicky et al. 1968). Centimetre-thick intercalations with gravel occur in several places near the top of the section and near its base, but their spatial extent is limited. Presumably, these were tongues of coarse clastics slumping from the surrounding elevations built of Paleozoic rocks.

Throughout the section, rare few-centimetre thick intercalations of sandstone occur. Irregular small pieces of coalified wood (probably fusinite) are also common (Figure 2(G)–(H)). They enable estimates of compaction of the sediment, apparently resulting in reduction of its original thickness more than six times.

The first feather-like fossil was found in Aulie in 1971 by Sharov, who referred to it on the museum label as ‘Praeornis.’ Its taxonomic description was published by Rautian (1978) and the formal name *Praeornis sharovi* (Rautian 1978) was introduced. The specimen is housed in the collection of the Paleontological Institute of the Russian Academy of Sciences, PIN 2585/32. We (TS and GN) had an opportunity to examine the fossil in 2008 and this allows its more detailed interpretation presented below, based on a series of digital photographs and interpretive sketches. The slab housed in Moscow is weathered and the original tissue is not preserved. In places where the tissue was voluminous, a network of dolomitic veins remained. Thinner parts of the specimen are recognisable as smooth areas on the slab.

The second specimen, initially interpreted as a plant fossil, was collected by our team in 2006 and is housed at the Institute of Palaeobiology of the Polish Academy of Sciences in Warsaw, ZPAL V 32/967. Both part (Figure 3)

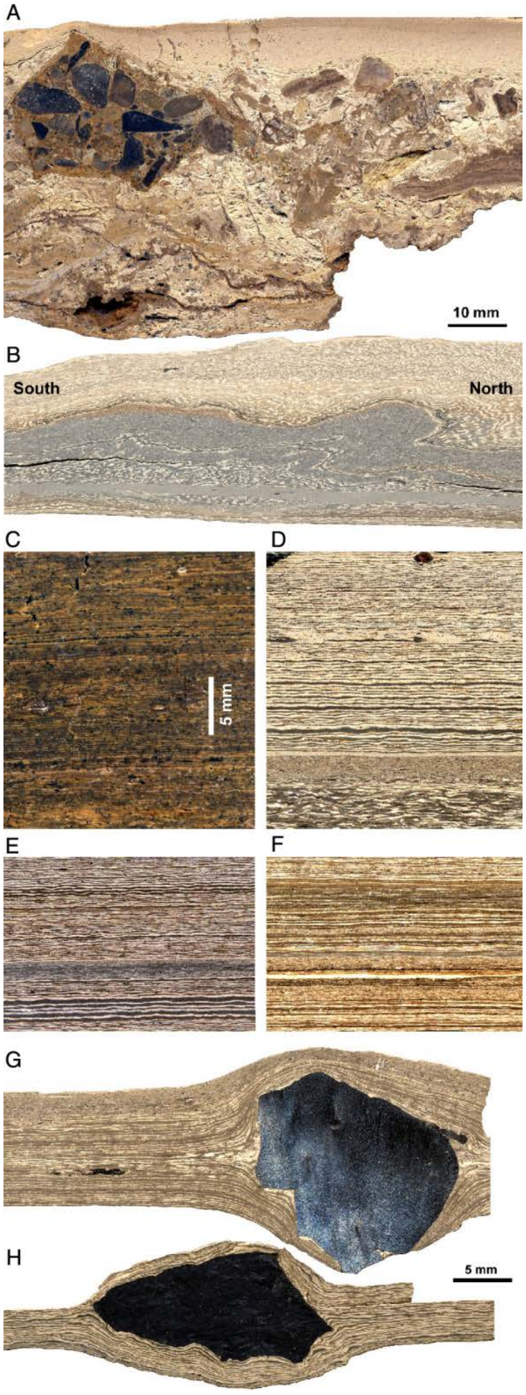

Figure 2. Polished rock samples from the Karabastau Formation at Aulie, Great Karatau, Kazakstan. (A) Sample 1 from near the top of section 3 (see Figure 1) with an angular piece of conglomerate and irregular lamination of presumably algal origin. (B) Section of slumping laminated shale from section 1. (C) Sample 2 in the upper part of section 3 (Figure 1); laminated dolomitic limestone. (D)–(F) Varieties of claystone with white dolomitic (presumably summer) and dark organic-rich (presumably wet season) laminae from section 1 and lower part of section 3. (G)–(H) Fusinite grains within laminated claystone showing degree of compaction of the surrounding rock.

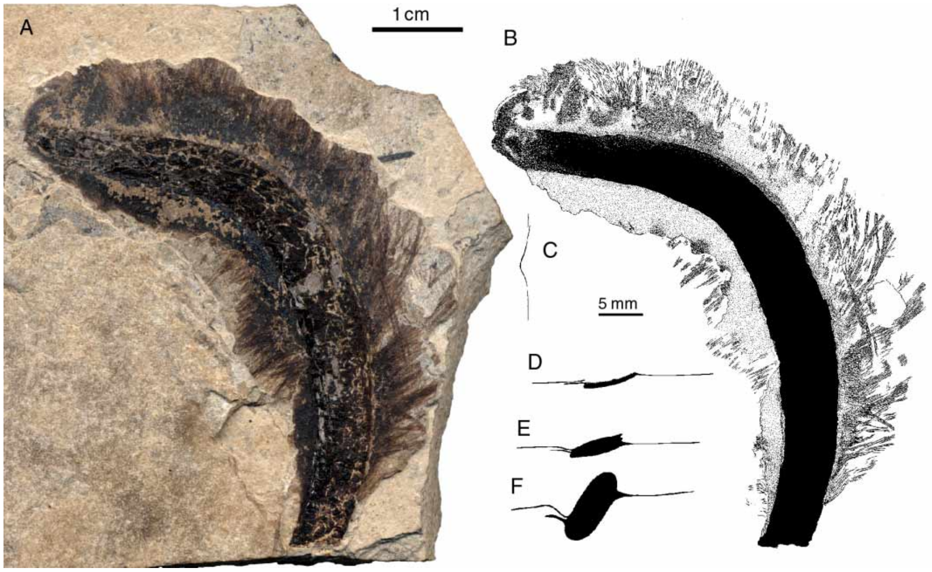

Figure 3. Putative ‘proto-feather’ ZPAL V 32/967 from the Karabastau Formation at Aulie, Great Karatau, Kazakstan. (A) Scan of the original specimen (part). (B) Camera lucida drawing. (C) Section across the distal portion of the specimen showing distribution of organic matter. (D) Section across the proximal portion of the specimen. (E) Composite section of part and counterpart. (F) Restored section prior to compaction. Note three ‘vanes’.

and incomplete counterpart were collected from the exposure wall (Figure 1(A)) and the black carbonised tissue is preserved intact, although cut by a network of numerous dolomitic veins. The most delicate organic structures are preserved as a darkening on the slab surface. The specimen is compressed, but its original 3D organisation is readable.

As usual for continental strata, it is not easy to find strong support for paleontological dating of the Karabastau Formation. Rasnitsyn and Zhang (2004), in their review of the hymenopteran fauna of the Chinese Daohugou Formation, concluded that its composition is intermediate between the early Late Jurassic assemblage of Karatau and assemblages from near the Lower/Middle Jurassic boundary. Liu et al. (2006) provided zircon U–Pb dating of the Daohugou Beds between 164 and 158 million years ago. Vršanský (2007) accepted this estimate, giving the Karatau fossils *ca.* 160 million years. Also, Zhang (2006) used insects to suggest the latest Middle Jurassic (Callovian) or earliest Late Jurassic (Oxfordian) ages for these formations.

Animal affinity of *Praeornis*

There are several aspects of the new specimen indicating that it represents the same kind of structure as the holotype of *Praeornis*. (1) The shaft in both the specimens does not taper distally; (2) its originally organic matrix is cut by a dense network of dolomitic veins, suggestive of early diagenetic contraction of the tissue; (3) the massive shaft (and its serial lateral extensions in the holotype) bears a thin membrane on sides and (4) a third vane supplement on the concave side of the shaft. We find it unlikely that such a series of similarities unknown elsewhere, developed by chance in different organisms represented by fossils from the same geological unit, thus co-occurring spatially and temporally with each other. Likely these are parts of the same kind of organism.

Bock (1985) suggested that the holotype of *Praeornis* is a cycad leaf rather than a feather. Nessov (1992) in his review of fossil birds was even more specific, indicating the leaf of *Cycadites sapportae* illustrated in Doludenko and Orlovskaya (1976, pl. 68:1–2) as conspecific with the Moscow specimen of *Praeornis*. Like other plant fossils at Aulie, this cycad specimen is preserved in a rather deep relief, with clear margins, which makes it rather unlike *Praeornis*, despite the general feather-like appearance. The main difference between *Praeornis* and plant fossils from the Karabastau Formation is that in plants the internal and external structure is generally well preserved, whereas the tissue of *Praeornis* shaft lacks any recognisable structuring. Leafs of cycads and conifers easily exfoliate intact from the rock surface. Their cuticle is smooth and hard. The original fibrosity of wood is preserved at least in places. In contrast, the carbonised tissue of the shaft in *Praeornis* breaks into glossy irregular pieces with conchoidal fracture. Numerous, chaotically oriented fissures separating those pieces are filled with dolomite. Apparently, the volume of the organic matter reduced significantly during diagenesis. Such preservation remains unknown in plants from Aulie.

Most authors dealing with fossil feathers follow Bock (1985) in rejecting avian interpretation of *Praeornis* (e.g. Kellner 2002). Glazunova et al. (1991) presented some observations of the specimen under SEM and supported its avian affinity, but because of weathering such evidence could not be conclusive. The mineral filling of the rachis in the Moscow specimen hardly has anything to do with its original structure.

Access to the original tissue of the rachis is offered by the new specimen of *Praeornis*, which has the shaft matrix represented by a black coalified substance. This enables geochemical studies and use of carbon-stable isotope as a tool for determining its biological origin. Depletion of heavy ^{13}C may be used to discriminate between plant and animal tissues because each metabolic turnover of organic matter enriches it in the light isotope ^{12}C. The δ^{13}C is a powerful tool for tracing nutrient flow within ecosystems (DeNiro and Epstein 1978) and bird feathers are widely used as the source of evidence (e.g. Yohannes et al. 2007).

To compare fossils of different origin, we took *Pagiophyllum* conifer leaves and fish skeletons from the same site and strata. This removes the bias potentially resulting from ecological differences or diagenetic alterations that may make data uncomparable, if they come from different places or geological epochs. Samples from the ganoid fish *Palaeonisculus* were taken from the skull and a carbonised tissue was scraped from between the ribs or scales in the body. The proto-feather matrix was taken from the lower part of the main shaft. Altogether, ten samples were processed.

The two samples taken from the proto-feather gave similar δ^{13}C values: −24.68‰ and −24.44‰. Samples taken from four fish specimens, although more variable, show a similar range of values: −24.67‰, −24.52‰, −24.23‰ and −25.07‰. However, the plant remains δ^{13}C values, although similar to each other (–25,73‰ – −25,91‰) depart from those obtained from animal tissues. This makes any plant relationship of *Praeornis* unlikely, supporting the structural evidence (Figure 4).

Morphology of the *Praeornis* specimens

Specimen PIN 2585/32 is incomplete, with distal and proximal ends, as well as the margin of their left vane extending outside the preserved portion of the slab (Figure 5). Only the right vane margin can be traced. The original length of the specimen was substantially more than the present 149 mm. It cannot be estimated by simple extrapolation because the width of both the shaft (rachis; about 4.6 mm) and the whole specimen (about 18.5 mm) does not directionally change along its whole length. Although the counterpart was not found and the spongy network of dolomitic veins covering the shaft is now strongly abraded, there is no doubt that the thickness of the shaft was originally substantial. The shaft is gently curved towards the left, apparently wider, vane, which extends from the shaft at its surface facing the viewer and in places its plane is slightly above of it. The left vane is much below, with the specimen surface clearly stepping down.

Almost so deep in the rock matrix as the left vane, on the right side of the specimen, yet another, third vane extends. It is exposed, owing to exfoliation of the external vane, only near the broken proximal end. Although clearly visible on Rautian's (1978) photographs, it was overlooked by him, probably because its presence does not fit the ground plan of an avian feather. The vane was thick and of uniform internal structure, as indicated by the spongy appearance of its interior. Its extent and shape outside the exposed area remains unknown.

As noticed and measured by Rautian (1978), the structures interpreted by him as barbs (rami) of the external left vane deflect from the shaft at lower angle (about 16°) than those of the internal vane (about 20°). If such homology is accepted as correct, the vanes asymmetry suggests that the specimen is a right-wing flight 'proto-feather'. Each 'barb' is represented by a band of spongy matrix, indicative of being a thick elevated structure. Thin blades on both sides of this spongy structure may correspond to series of barbules in the avian feather, but there are no signs of the blade being split into separate units. No structure is recognisable in those blades, probably because the organic matter that could express it in colouration weathered out. The 'barb' is of uniform thickness for most of its length, but near its tip both the 'barb' and lateral blades gradually narrow. The 'barb' tips are thus acute.

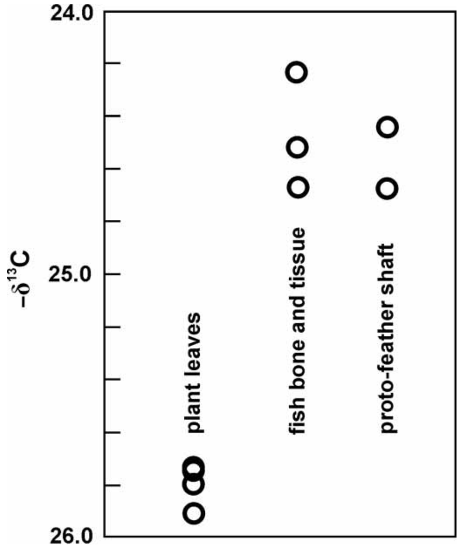

Figure 4. Comparison of δ^{13}C values for various fossils from the Karabastau Formation at Aulie, Great Karatau, Kazakhstan. Note that all measurements were taken from specimens collected at the same site and from the same rock unit and that values for plant and animal material widely diverge, even if few available specimens prevent statistical treatment of the sets of samples.

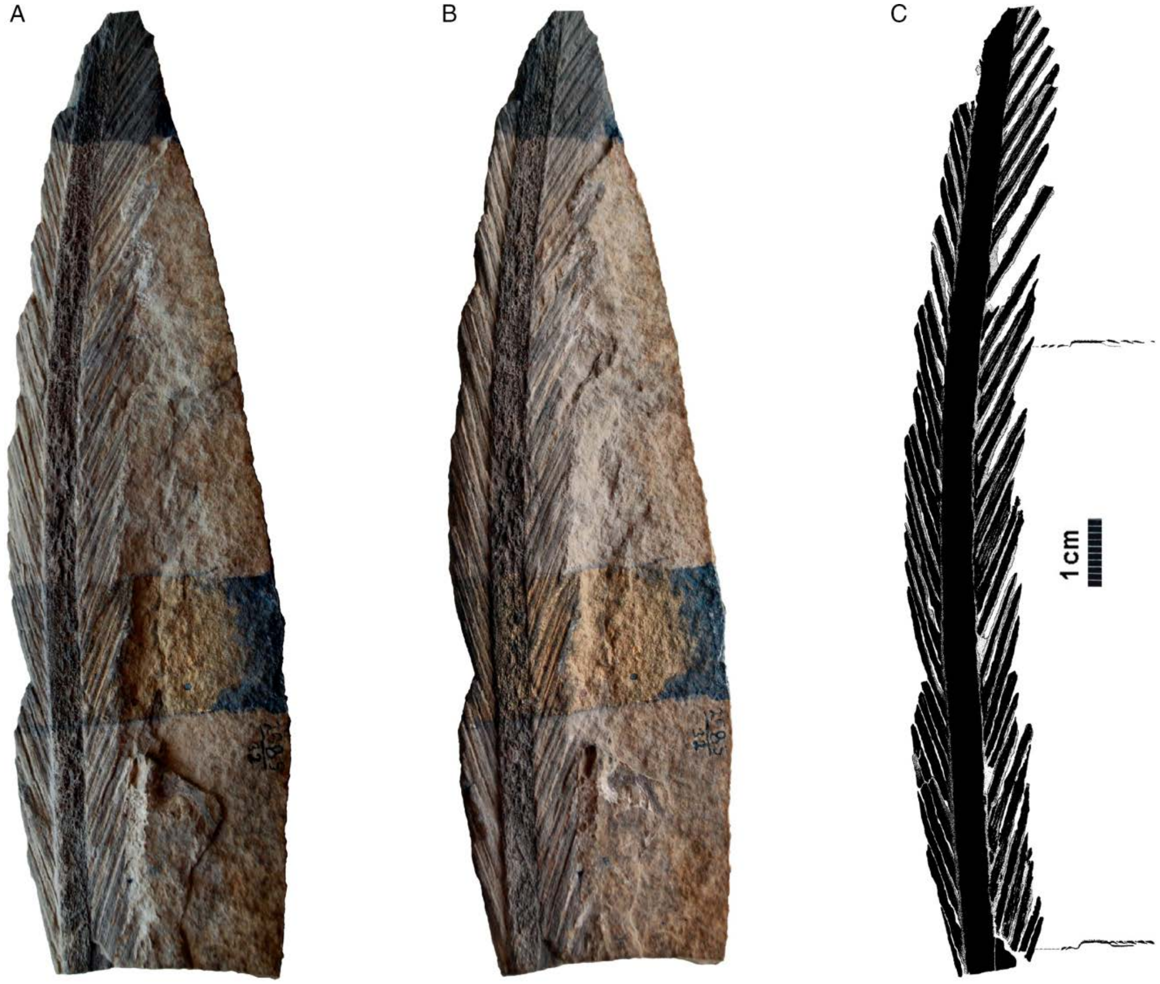

Figure 5. Holotype PIN 2585/32 of *Praeornis sharovi* Rautian, 1978 from the Karabastau Formation at Aulie, Great Karatau, Kazakhstan. (A) (B) Specimen photographed with light from upper left and upper right, respectively. Black and/or golden bands are artefacts – coatings for SEM. (C) Drawing traced from a composite digital photograph and semi-diagrammatic sections across the proximal and distal parts.

Overlapping of each distal ‘barb’ by a blade emerging from its proximal neighbour at both left and right ‘vanes’ indicates that the visible surface of the Moscow specimen is the dorsal one. It is thus yet another argument for interpreting it as the right-side feather.

The new specimen ZPAL V 32/967 is better preserved and more complete than the holotype. Its black carbonised shaft is of almost uniform width along its whole length, although near the base it is about 6 mm thick, and in the mid-length about 8 mm, narrowing to 5.5 mm near the tip. This narrowing may be due to deformation and migration of the line of attachment of the external vane, however. This is suggested by the rounded outline of the shaft tip, which submerges externally under the vane. The actual outline of the shaft may thus be club-like, with its width gradually enlarging till the rounded tip (Figure 6). The most proximal part of the shaft is elevated in its centre, but not due to its thickness. Instead, it thins there and the appearance of the shaft was probably somewhat conical.

The proximal end of the shaft is preserved in the rock as irregularly broken (or cut) prior to deposition. There is no narrowing near its tip, as typical for calamus of the present-day feathers (and also of *Archaeopteryx*; Figure 7). The *Praeornis* feather was thus an extension of a surface sclerotic (perhaps keratinous) structure, more like reptilian scale than modern feather.

Both the Moscow specimen and the new one bear three vanes. The additional vane on the concave side of the shaft is of a rather homogenous internal structure and was probably narrower. The two others have a fibrous internal structure. The fibres are generally parallel to each other and extend almost perpendicular to the axis on its concave side but with the angle changing from roughly 30° near the base to perpendicular in the distal portion of the specimen (Figures 3 and 6). Bunches of a few fibres each tend to split

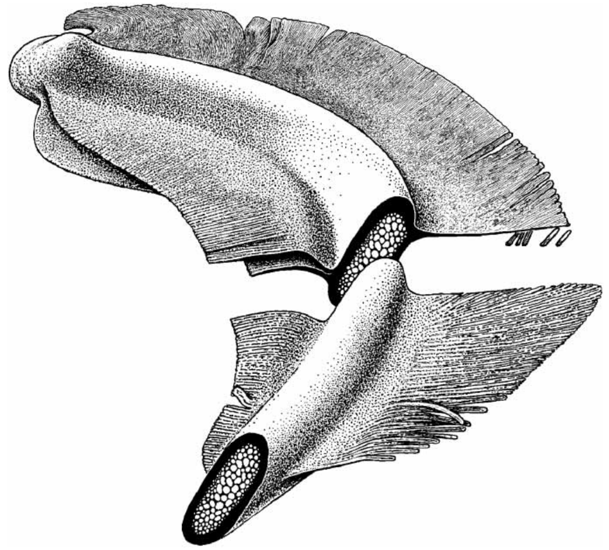

Figure 6. Restoration of the proto-feather ZPAL V 32/967 from the Karabastau Formation at Aulie, Great Karatau, Kazakstan.

from others in the marginal part of the external vane. They are strongly bent and interfingering in places. Near the tip of the specimen, there is a whirl of fibres with their orientation towards the base of the rachis near their point of attachment and then curving towards the rachis tip. Possibly, the vane base first migrates closer to the axis of the rachis in its course along the shaft, and then curves along the margin of its tip.

If one attempts to homologise structures in the two specimens, the dark striae-crossing vanes of the new one possibly correspond to robust structures of the holotype interpreted by Rautian (1978) as barb axes. The parallel dark lines in the new specimen would then represent rows of keratinised cells that did not concentrate into compact units.

Judging from the available morphological evidence, at the moment there is hardly any reasonable alternative to the Rautian's (1978) interpretation of *Praeornis*. Parallel fibres can be found in gill structures of various animals but nothing fits such interpretation in the Karatau Jurassic lake fauna. The largest of associated fish are still of body size comparable with single *Praeornis* specimens, and they do not preserve gills or cartillagineous gill arches. Cartillage is represented neither in amphibians nor in reptiles of the Karabastau Formation and it is unlikely that its fossilisation would result in the voluminous carbonised structure characteristic for both *Praeornis* specimens. Most likely, these are sclerotic appendages with at least remote relationship to bird feathers or reptilian scales. In either case, an enigmatic aspect of *Praeornis* is the presence of three vanes.

Conclusions

Feathers in all present-day birds develop from a cylindrical dermal papilla (Prum 1999, 2005; Prum and Brush 2002), with apoptosis involved in formation of their complex pennate structure (Chang et al. 2004). Such was probably also the organisation of the feather of *Archaeopteryx* with its narrowing rachis. The shape of rachis of *Praeornis*, with its oval cross-section, is not inconsistent with the idea forwarded by Prum (1999) that the first feather originated as a cylindrical structure, then transformed into a tuft of unbranched barbs, the status of a flat bipennate feather being the most advanced. But, this is not the position of *Praeornis* proposed for it in its original description by Rautian (1978).

The new finding of *Praeornis* 'proto-feather' adds some credibility to Rautian's (1978) scenario of the origin of feathers. Rautian (1978) interpreted lateral pennate ramifications of the *Praeornis* shaft as barbs, and the membrane on their sides as an evolutionary Anlage of barbules and hooklets of advanced feathers. He proposed also a hypothetical stage ancestral to *Praeornis*, with acute shaft backed on sides only by membranes. This would be

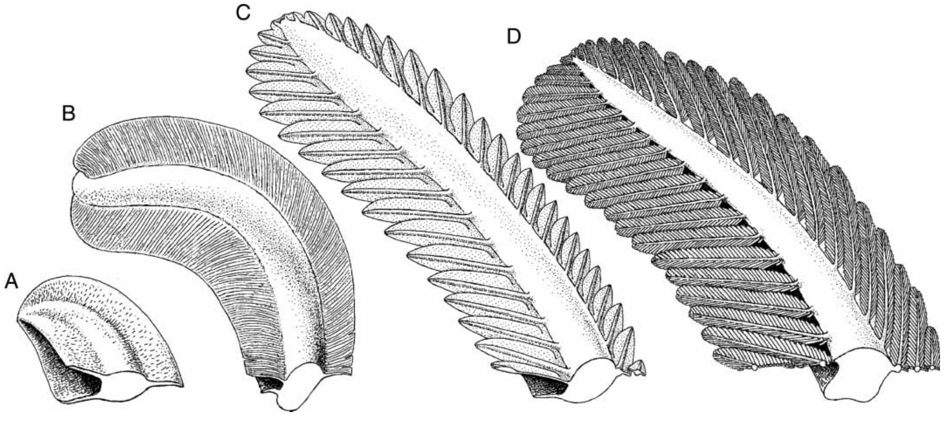

Figure 7. Proposed homology and scenario of transformation of a hypothetical scale arming a body ridge (A) into cover and contour proto-feathers of *Praeornis* with three vanes (B) and (C) and an avian feather with tetragonal shaft (D).

consistent with the opinion of Maderson and Alibardi (2000) that 'a proto-feather and its follicle are most easily derived from isolated, flattened, elongated, reptilian scales'. The new specimen attributed here to *Praeornis* roughly fits this idea but the question immediately emerges, for what purpose more than two vanes developed in the putative scale ancestral to the 'proto-feather'.

A possible explanation may be found in the location of prominent integumental structures on bodies of reptiles preceding *Archaeopteryx* and *Praeornis*. One may imagine transformation of a scale with a Λ-shaped cross-section into an asymmetric structure of λ-shaped section, finally losing the third vane (Figure 7). In subsequent expansion of proto-feathers to the skin surface earlier covered by regular scales, the same morphogenetic factory developed was used to create the cover proto-feathers. Their axes had to be rotated 90° to arrange them in a scale-like pattern. One may guess, that to allow for rotation, their base attained cylindrical shape. Such a complex course of evolutionary transformation of the original scale into a feather may be the reason of its puzzling mode of organogenesis.

Prominent scales armed the ridges along the back and posterior margins of limbs in the Late Triassic probable megalancosaurid *Longisquama* (Sennikov 2008). Although their original organic tissue was apparently replaced with a clay mineral, which resulted in disparate interpretations of their nature (Sharov 1970; Jones et al. 2000; Reisz and Sues 2000; Peters 2000; Unwin and Benton 2001; Voigt et al. 2009), it is clear that they were rather robust proximally but very thin and wide at their distal ends. These scales were compressed from their sides, not parallel to the body surface. Their plane appears thus perpendicular to the plane of a regular reptilian scale, although scales of similar shape develop along the back of recent iguanas. Homology of *Longisquama* scales with feathers, proposed by Jones et al. (2000), met a vivid opposition from many authors (Prum 2001; Stokstad 2001) and more convincing evidence for the proto-feather stage is clearly necessary. At the moment, the three dimensionally and structurally preserved *Praeornis* possible 'proto-feathers' remain the main source of evidence to fill the gap between them and *Archaeopteryx*.

Acknowledgements

The expedition to the Karatau Range, Kazakstan in 2006, organised by us as a joint venture of the Instytut Paleobiologii PAN, Warsaw, and K.I. Satpaev Institute of Geological Sciences, Almaty, was partially supported by a grant from the SUBIN programme of the Fundacja na rzecz Nauki Polskiej. Dmitry V. Malakhov was our guide and the main organiser. We thank the authorities of the Palaeontological Institute of the Russian Academy of Sciences, Moscow, for permission to examine and photograph the holotypes of *Praeornis* and *Longisquama*. Michael Buchwitz (Bergakademie Freiberg) allowed us to examine his newly collected specimens of *Longisquama*.

Isotope measurements were done by Michael Joachimski in the Stable Isotope Laboratory, Department of Geology, University of Erlangen-Nürnberg, Erlangen, Germany, and supported financially from a grant to Grzegorz Pieńkowski (Polish Geological Institute, Warszawa, Poland).

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