Integumentary Structures in *Kulindadromeus zabaikalicus*, a Basal Neornithischian Dinosaur from the Jurassic of Siberia

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4.1 Introduction

Pre-1998, feathers were thought to be an exclusively avian characteristic, shared by all birds and extending back to the earliest representative of the clade, *Archaeopteryx*, in the Late Jurassic, ca. 150 million years ago (Witmer 2009). Since the description of *Sinosauropteryx* (Ji and Ji 1996; Chen et al. 1998), Middle-Late Jurassic and Early Cretaceous deposits from northeastern China have yielded numerous theropod dinosaurs bearing simple filamentous "protofeathers." Further, true pennaceous feathers featuring a rachis (shaft) and vanes were reported in nonavian pennaraptoran theropods that are closely related to birds (e.g., Xu et al. 2001, 2003; Hu et al. 2009; Godefroit et al. 2013). These discoveries of feather-like structures in theropods are consistent with current understanding of the evolutionary origin of birds, which are now almost unanimously regarded as representatives of the theropod and maniraptoran clades.

Subsequent reports of projecting, possibly hollow, bristle-like structures on the tail of the basal ceratopsian *Psittacosaurus*, also from the Early Cretaceous of Liaoning Province in northeastern China (Mayr et al. 2002, 2016), raised the possibility that filamentous epidermal structures may have been present in a broader clade that includes ornithischian dinosaurs. Patches of long filaments, reminiscent of structures present in theropods and thought to be the evolutionary precursors of feathers, were subsequently described in the heterodontosaurid ornithischian *Tianyulong*, from the Middle-Late Jurassic Yinliao Biota of Liaoning Province (Zheng et al. 2009; Sereno 2012). Whether these filaments in ornithischian dinosaurs are epidermal in origin, or represent remains of dermal collagen fibers, however, has been disputed (Lingham-Soliar 2010a, b; Mayr 2010). Even if these filaments can be confirmed as representing

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epidermal structures, it is still unclear whether these simple monofilaments are part of the evolutionary lineage of feathers, or represent independent evolution of projecting epidermal appendages (Witmer 2009; Barrett et al. 2015).

The discovery of *Kulindadromeus zabaikalicus* from the base of the Ukureyskaya Formation (Middle Jurassic; Cincotta et al., 2019) of Kulinda (Cherynyshevsky District of Chita Region, southeastern Siberia, Russia) sheds light on the origin and early diversification of integumentary appendages in dinosaurs. Various epidermal structures are well preserved adjacent to, and sometimes directly associated with, the skeletal elements. These include small scales along the distal tibia and on the foot, larger imbricated scales on the tail, long unbranched filaments on the head and thorax, and compound "protofeather"-like structures on the humerus, femur, and the proximal part of the tibia (Godefroit et al. 2014a). Given the position of *Kulindadromeus* near the evolutionary base of ornithischian dinosaurs, the presence of not only monofilaments, but also of branched epidermal structures, suggests that compound feather-like structures were potentially widespread among the whole dinosaur clade, or at least within the Ornithoscelida (Theropoda + Ornithischia) clade according to Baron et al.'s (2017) recent phylogenetic classification of dinosaurs. Here we describe in detail the integumentary structures in *Kulindadromeus zabaikalicus* and discuss their potential function and importance for dinosaur evolution.

4.2 Geological Setting and Taphonomy of the Kulinda Locality

The Kulinda locality is in the Chernyshevsky District of the Chita Region (Zabaikalsky Krai), about 220 km to the east of Chita city (Fig. 4.1).

Fig. 4.1 Location of Kulinda dinosaur locality (Chitinskaya Oblast, Russia). Inset map: Zabaikalsky Krai (in yellow)

The site was discovered by Sofia M. Sinitsa and her team from the Institute of Natural Resources, Ecology, and Cryology, Siberian Branch of the Russian Academy of Sciences, while they were conducting a geological survey in the Olov Depression along the Kulinda River, close to Chernyshevsk village (Sinitsa 2011). Four trenches in the lower part of the Ukureyskaya Formation revealed a succession of massive and alternating sandstones, siltstones, tuffaceous sandstones, tuffaceous siltstones, and tuffites. Based on comparisons of the paleoentomological and the microfaunal contents with the Glushkovo Formation in the Unda-Daya Depression, the Ukureyskaya Formation has been dated as Late Jurassic–Early Cretaceous (Sinitsa and Starukhina 1986; Sinitsa 2011). However, new U-Pb ages, together with palynological data, provide evidence of a Bathonian age—between 168.3 ± 1.3 Ma and 166.1 ± 1.2 Ma—for *Kulindadromeus* (Cincotta et al. 2019). Three fossiliferous horizons rich in ornithischian skeletal remains have been excavated to date at Kulinda, one in each of trenches 3 and 4, and an additional bonebed between those trenches (Fig. 4.2).

Bonebed 3, in trench 3, is 100–200 mm thick and consists of well-preserved disarticulated bones within a gray, silty matrix. Articulated elements and integumentary structures are rare. The sediments in trench 4 are probably slightly older than those in trench 3. Bonebed 4 comprises finely laminated, organic-rich claystone. Some of the bones in this horizon are articulated, and delicate integumentary structures are preserved as a thin film of carbonaceous material. This horizon was deposited in a quiescent environment far from clastic sources. The matrix of this bonebed is highly indurated, and laminae are occasionally deformed; some skeletal elements are preserved as external molds. This contrasts with the lithology and style of preservation of the material from bonebed 3 and suggests localized chemical environments during diagenesis.

Trench 3-3, between trenches 3 and 4, has been excavated since 2012. The section mostly contains fine-grained deposits (siltstones) along with poorly sorted sandstones and breccia. Seven fossiliferous layers with bone remains have been identified so far. The bone material is dominated by vertebrae, pelvic, and limb bones. Soft tissues are rather rare although faint traces of protofeathers are present, along with well-preserved scales.

Most fossils discovered in bonebeds 3, 3-3, and 4 belong to small individuals, most likely juveniles or sub-adults; larger individuals are rare. The overrepresentation of younger individuals in the bonebeds could suggest an attritional accumulation of carcasses leading to the formation of the bonebeds and not a single catastrophic event (Lyman 1994). Confirmation of this hypothesis requires a detailed age-frequency distribution of the long bones and further taphonomic investigation.

4.3 Biodiversity of the Kulinda Dinosaur Fauna

Most of the skeletal elements recovered from the three bonebeds at Kulinda are isolated or only partially articulated. The integumentary elements typically occur as isolated patches but can be directly associated with the skeletal elements. These features hamper attempts to reconstruct the skeleton and the external aspect of *Kulindadromeus*, and to estimate the taxonomic diversity of the bonebed material.

Except for a single shed tooth from a medium-sized theropod (which was found in bonebed 3), Godefroit et al. (2014a) hypothesized that the bonebeds at Kulinda are monospecific: detailed analysis of the skeletal elements (in particular, the partially articulated remains) preserved within and between the bonebeds reveals no evidence for multiple taxa of basal ornithischians in the Ukureyskaya Formation of the Kulinda locality. Each individual skeletal element is represented by a single morphotype; all the observed minor differences can easily be explained by ontogenetic and normal intraspecific variations.

Kulindadromeus zabaikalicus was a small, 1.5 m long, bipedal herbivore with a short skull, teeth adapted for herbivory, short forelimbs and elongate hindlimbs and tail (Fig. 4.3). Phylogenetic analysis (Fig. 4.4) recovers *Kulindadromeus* as a

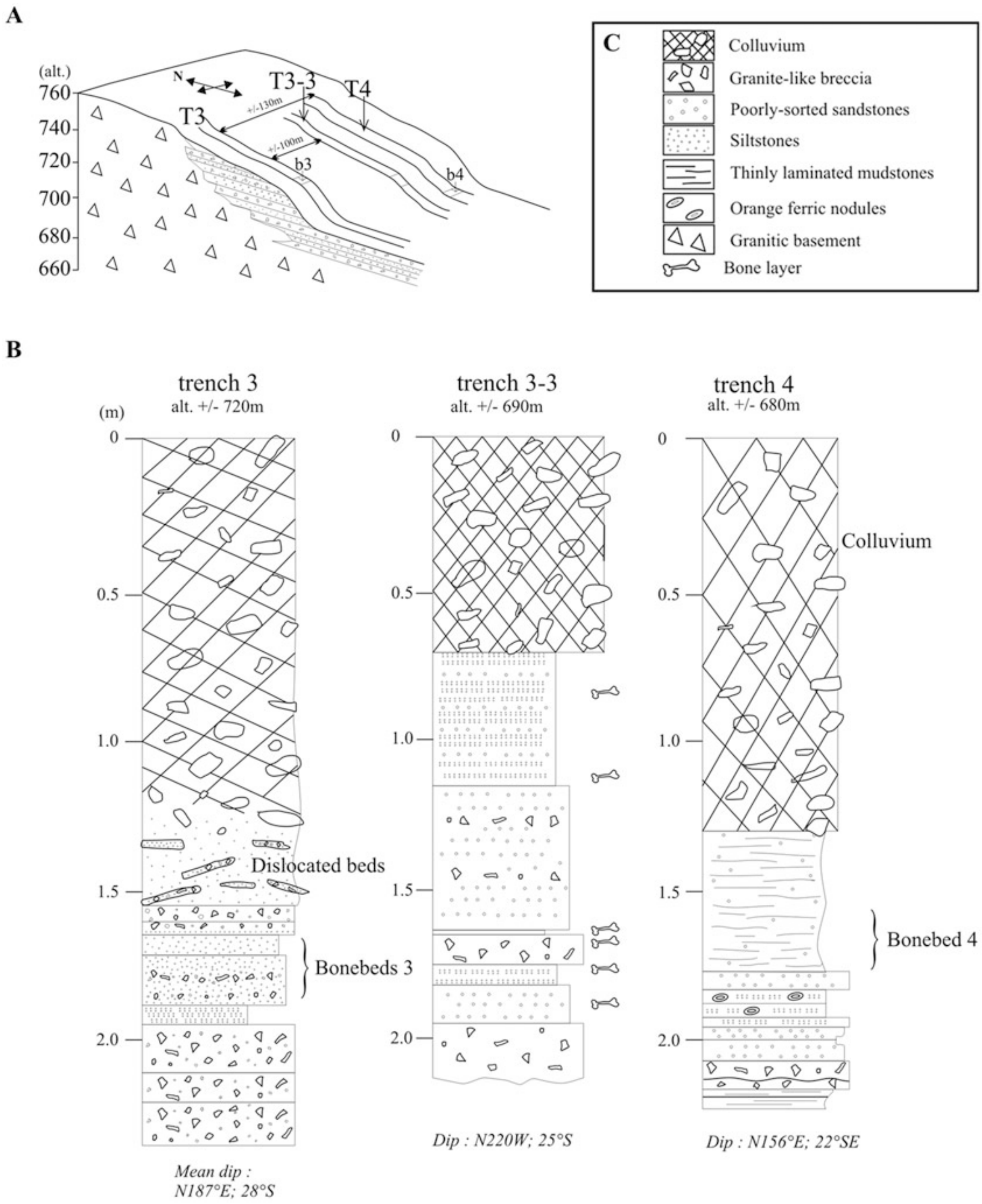

Fig. 4.2 (**a**) Schematic positioning of the trenches (T3, T3-3, and T4) and of the bonebeds (b3 and b4) at the Kulinda dinosaur locality, Ukurey Fm (Middle to Late Jurassic); (**b**) lithological logs of the sediments in trenches 3, 3-3, and 4, with the positions of the bonebeds. Bonebed 4 was only identified in the south front of trench 4; (**c**) lithological legend of the figures

basal member of Neornithischia (all genasaurians more closely related to *Parasaurolophus walkeri* than to *Ankylosaurus magniventris* or *Stegosaurus stenops* [Butler et al. 2008]) and the sister taxon for Cerapoda (*Parasaurolophus walkeri*, *Triceratops horridus*, their most recent common ancestor and

Fig. 4.3 Osteological reconstruction of *Kulindadromeus zabaikalicus*. Model by Jonica dos Remedios Esteves

all descendants [Butler et al. 2008]) (Godefroit et al. 2014a).

Alifanov and Saveliev (2014, 2015) proposed an alternative interpretation for the dinosaur fauna at Kulinda and named three new taxa from this locality: the 'hypsilophodontian' ornithopods *Kulindapteryx ukureica* and *Daurosaurus olovus* (Alifanov and Saveliev 2014), and the 'nqwebasaurid' ornithomimosaur *Lepidocheirosaurus natalis* (Alifanov and Saveliev 2015). Detailed description of the osteology of the dinosaurs from Kulinda is beyond the scope of this chapter, but some brief comments are made below.

Alifanov and Saveliev (2014, 2015) do not apply modern taxonomic standards for elaborating their classification schemes: they do not use cladistic methods for inferring the phylogenetic relationships between taxa. *Kulindapteryx* and *Daurosaurus* only differ in the structure of their ischia, but those differences can easily be explained by differences in the preservation and orientation of the bones, falling within the intraspecific variation of the *Kulidadromeus zabaikalicus* hypodigm.

Per Alifanov and Saveliev (2015), the caudal vertebrae and associated scales referred by Godefroit et al. (2014a) to *Kulindadromeus zabaikalicus* belong to a new ornithomimosaur, *Lepidocheirosaurus natalis*. This interpretation is based on analysis of one partially articulated manus and caudal vertebrae associated by caudal scales. The caudal vertebrae show a spool-shaped centrum, well-developed postzygapophyses and weakly developed neural spines; these features are characteristic of theropods and contrast with the vertebrae of bipedal Ornithischia, which possess neural spines, a cylindrical centrum and weakly developed postzygapophyses. However, Alifanov and Saveliev's (2015) interpretation is apparently based on direct comparisons with the ornithopod *Hypsilophodon foxii* and lacks a broader phylogenetic context. For example, caudal vertebrae of more basal ornithischians, e.g., the heterodontosaurid *Tianyulong confuciusi* (see Sereno, 2012, fig. 25), closely resemble those discovered at Kulinda: from about the tenth vertebra, the centrum is elongate and spool shaped in lateral view, the neural spines are reduced to a ridge, and both the pre- and postzygapophyses are long, extending beyond the level of the articular surfaces of the centra. Except for the absence of evidence for ossified tendons, the caudal structure in *Tianyulong* is remarkably similar to that in dromaeosaurid theropods (Sereno 2012) Furthermore, the hand of *Lepidocheirosaurus natalis*

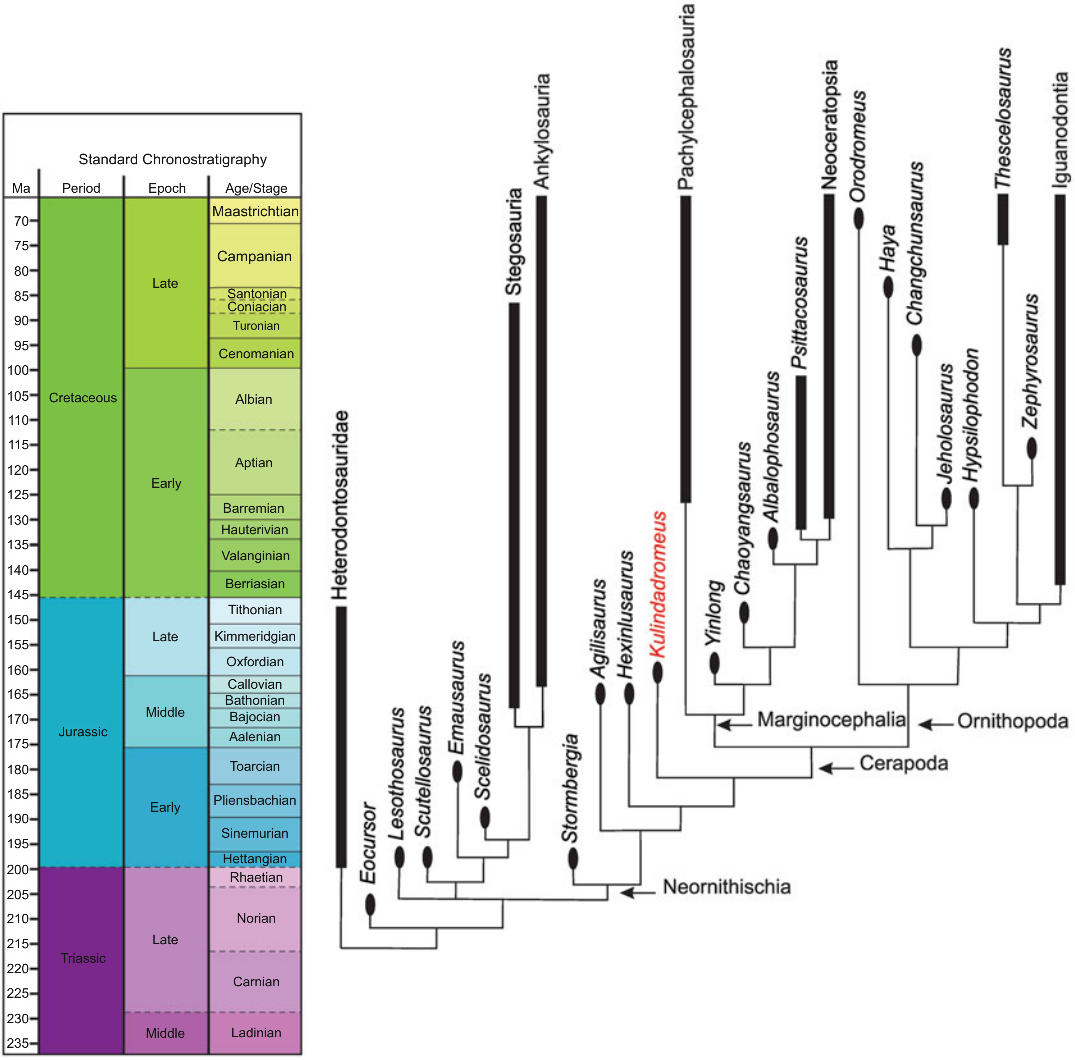

Fig. 4.4 Phylogenetic relationships of *Kulindadromeus zabaikalicus* among ornithischian dinosaurs (after Godefroit et al. 2014a). Time-calibrated strict consensus tree of the four most parsimonious trees (tree length = 571; consistency index excluding uninformative characters = 0.42; retention index = 0.7). In this hypothesis, *Kulindadromeus* is the sister-taxon of Cerapoda

from Kulinda closely resembles that of *Tianyulong* (see fig. 27 in Sereno 2012). Combined, these observations strongly indicate a lack of support for the hypothesis that basal ornithomimosaurs were present at Kulinda and that the caudal and manus material described by Alifanov and Saveliev (2015) can be confidently attributed to basal ornithischians, such as *Kulindadromeus zabaikalicus*.

The most parsiminous interpretation of the Kulinda bonebeds is thus that they represent accumulation of a monospecific dinosaur assemblage, as hypothesized by Godefroit et al. (2014a).

4.4 Diversity of Epidermal Structures in *Kulindadromeus*

The various epidermal structures preserved in *Kulindadromeus* are discussed below.

Pedal and Manual Scales Small (3.5–5 mm long) imbricated and hexagonal scales that resemble the scutella in modern birds (Lucas and Stettenheim 1972) are associated with the distal part of the tibia and usually show high relief (Fig. 4.5d). Smaller (<1 mm long), rounded, and nonoverlapping scales occur around the tarsus (Fig. 4.5d), metatarsus, and pes (Fig. 4.5e); these resemble the reticula along the plantar face of the pes in modern birds (Lucas and Stettenheim 1972). In INREC K4-6a-18/35 (part and counterpart of the same specimen), thick hemispherical pads, covered by tiny rounded reticula, occur on the ventral side of the manual phalanges, with one pad corresponding to each phalanx. A ventral pad is also present below the proximal part of the unguals of digits I and II (Fig. 4.5a–c). Similar pads are also present in *Concavenator* (Cuesta et al. 2015) and *Psittacosaurus* (Vinther et al. 2016).

Alifanov and Saveliev (2015) described similar reticulate scales around the manus of PIN 5395/1 ('*Lepidocheirosaurus natalis*'), herein tentatively referred to *Kulindadromeus zabaikalicus*. These authors also described a series of eight wide crescentic scales, approximately 1.5–2 times as wide as the corresponding phalanges, on phalanges I-1, III-2, and 3 and on metacarpal I. These scales abut but do not overlap. Similar scales occur on the scuta on the dorsal side of the metacarpus and pes in modern birds (Lucas and Stettenheim 1972). The crescentic scales in the fossils therefore likely covered the dorsal side of the phalanges, whereas the smaller reticulate scales likely covered the ventral side of the manus (*contra* Alifanov and Saveliev 2015).

Pad-like scaled structures also occur in bonebeds 3/3 and 4 but are not associated with skeletal material. The pads preserve tiny (<0.5 mm) reticulate scales that are organized into thin parallel sinuous lines, e.g., in specimen INREC K3/3-4-628 (Fig. 4.5f). The taphonomic conditions responsible for the formation of the Kulinda fossil locality were clearly conducive to the exceptional preservation of exquisite soft tissue structures (*contra* Lingham-Soliar 2014).

Scutate Caudal Scales The tail of *Kulindadromeus* was surrounded by a dozen longitudinal rows of scales (Figs. 4.6 and 4.7). It is, however, unclear whether the ventral side of the tail was completely covered by this scaly armor. The largest scales (ca. 20 mm long and 10 mm wide) occur along the proximal part of the tail. The paired dorsal series comprises scales that are significantly larger, and with a more complex morphology, than the lateral series. The caudal scales of *Kulindadromeus* are thin (<100 μm thick) and unornamented, and the dorsal series are slightly imbricated. Those caudal scales are clearly different from the thicker, usually sculptured, and nonoverlapping osteoderms in thyreophoran ornithischians and from the proportionally thicker and smaller scales in iguanodontian ornithopods (Bell 2012). Instead, the caudal scales of *Kulindadromeus* more closely resemble the epidermal scutae that cover the dorsal side of the metatarsus and pes in modern birds (Lucas and Stettenheim 1972). The preservation of the scales as carbonaceous remains does not support their interpretation as osteoderms because the bones (which also comprise calcium phosphate *in vivo*) clearly differ in their mode of preservation.

Scales from the paired dorsal series are arched and rectangular, whereby each scale covers a small part of the adjacent distal one (Fig. 4.6c, e, f). In the distal part of the tail, three scales from each series cover one vertebra (Fig. 4.6b). The proximal dorsal scales are much wider mediolaterally than long proximodistally. Some paired proximal dorsal scales are apparently fused along the median axis of the tail (Fig. 4.6c). Distal dorsal scales are proportionally narrower mediolaterally throughout the series. Notably, each scale from the paired dorsal series forms a triangular proximal spur that covers part of the preceding scale, forming a clip-like system that connects adjacent elements (Fig. 4.6e). Proximally, near the base of the tail (Fig. 4.6c), the dorsal scales are progressively smaller, more rounded, and do not overlap.

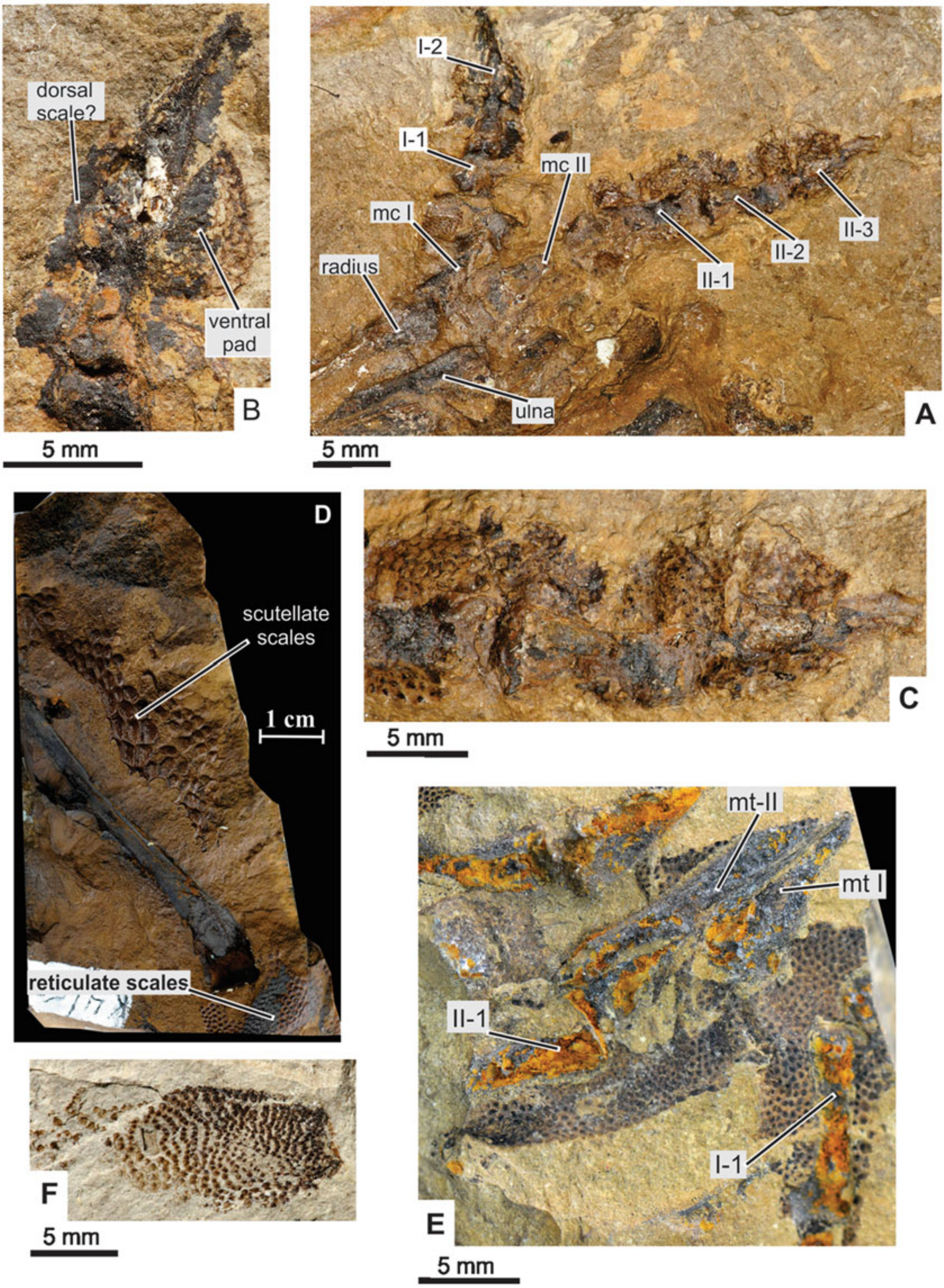

Fig. 4.5 Scales on the appendicular skeleton of *Kulindadromeus zabaikalicus*. (**a**) Scales around the right manus (INREC K4/6a-18); (**b**) close-up of the distal part of right digit I (INREC K4/6a-18); (**c**) close-up of the distal part of the right digit II (INREC INREC K4/6a-18); (**d**) scales around the distal tibia and around the tarsus (INREC K4/57); (**e**) scales around the right metatarsus and pes (INREC K4/118); (**f**) isolated pad-like reticulate structure (INREC K3/3-4-628). *mc* metacarpal, *mt* metatarsal

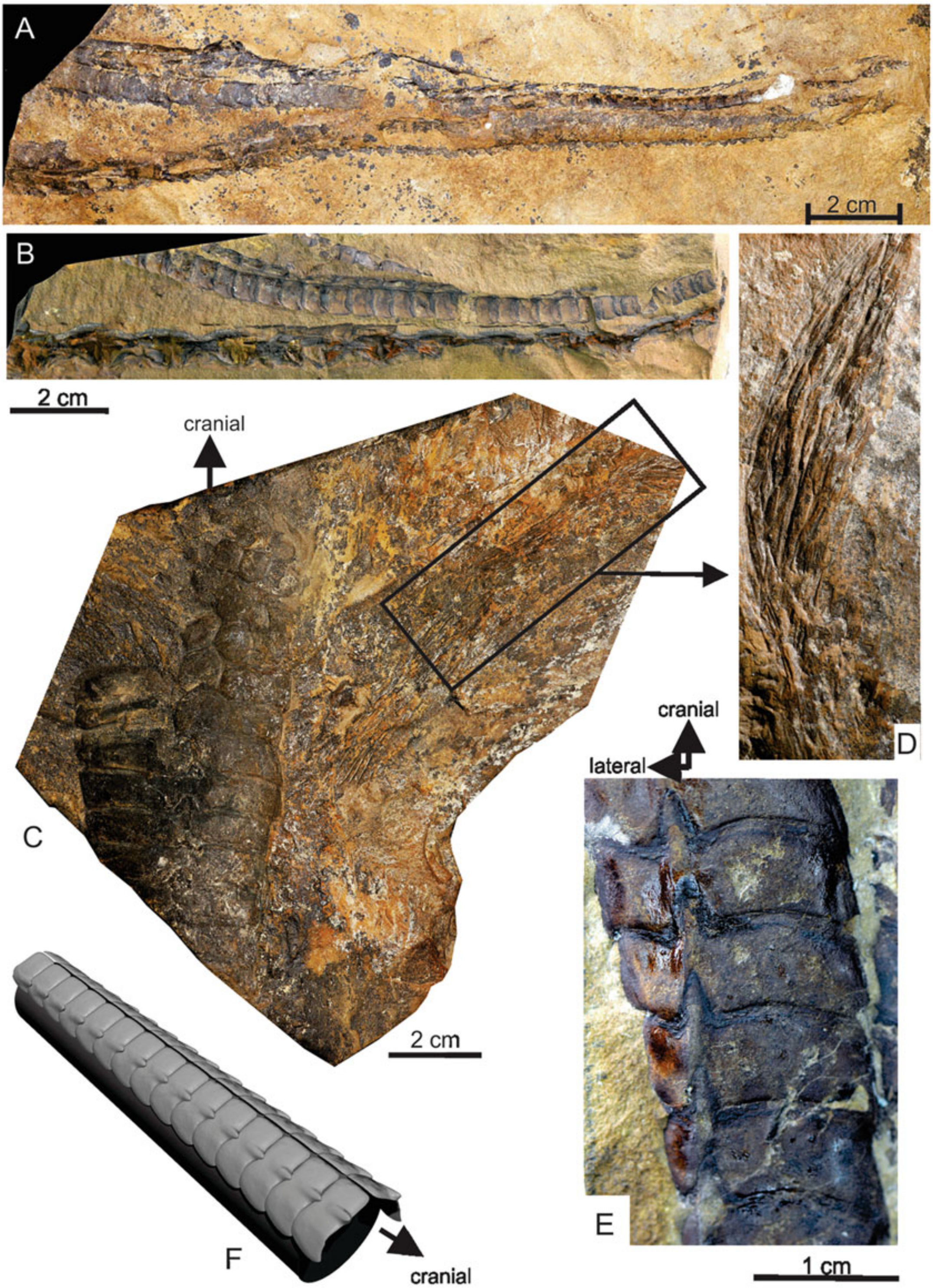

Fig. 4.6 Scales around the tail of *Kulindadromeus zabaikalicus*. (**a**) Scales around distal portion of the tail in left lateral view (INREC K4/5-6-127); (**b**) distal caudal vertebrae (left lateral view) and displaced dorsal scales (ventral view) (INREC K4/159); (**c**) double row of dorsal scales above the proximal part of the tail (INREC K4/9-41) in dorsal view; (**d**) close-up of ventral bundles of bristle-like structures (INREC K4/9-41); (**e**) close-up of the left dorsal row of caudal scales (INREC K4/117) in dorsal view; (**f**) partial reconstruction of the caudal scales in laterodorsal view

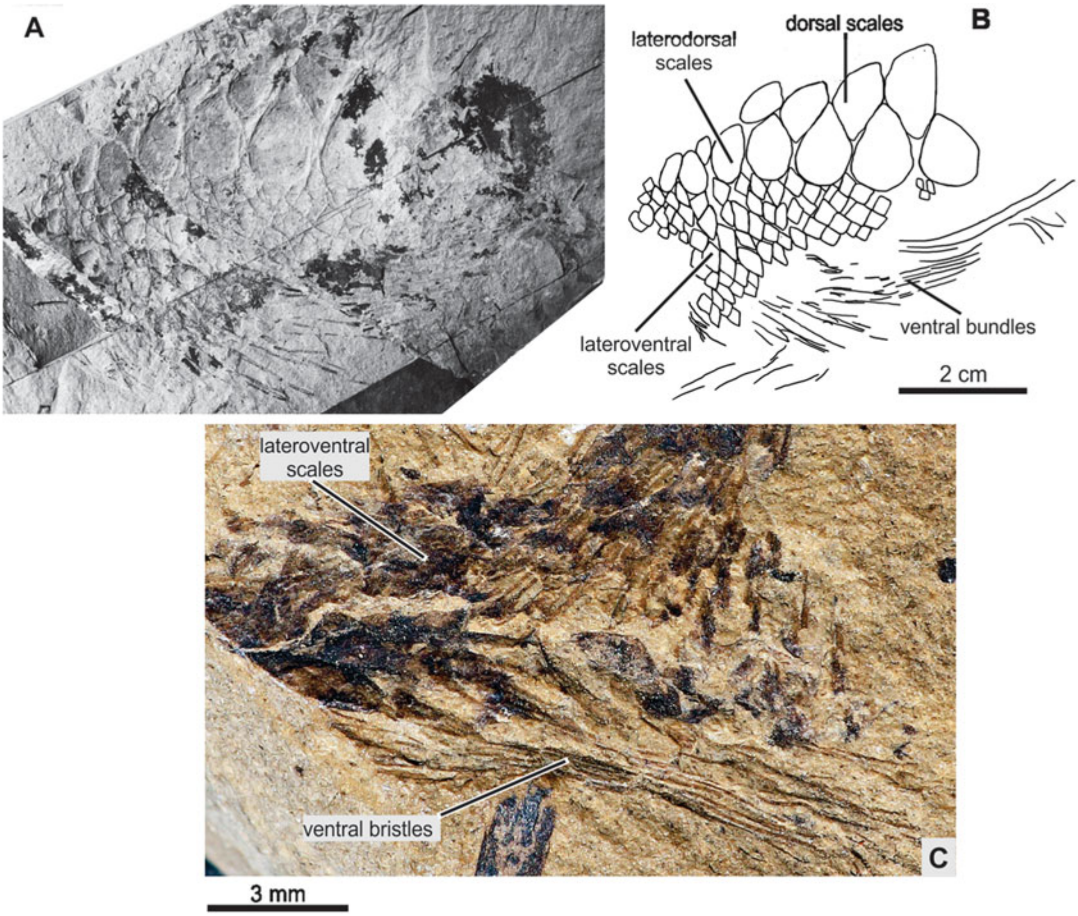

Fig. 4.7 Scales around the tail of *Kulindadromeus zabaikalicus*. Photograph (**a**) and interpretative drawing (**b**) of the right lateral side of a partial tail armor (INREC K3-3/95); (**c**) close-up of lateroventral scales (INREC K4/6d-1), showing the ventral bristle-like structures

The scales from the dorsolateral series are significantly narrower dorsoventrally (or mediolaterally) than the corresponding scales of the dorsal series (Fig. 4.7a, b). The ventral border of the dorsolateral scales is rounded, whereas their dorsal border is triangular, so each lateral scale imbricates between adjacent dorsal scales. The number of dorsolateral scales therefore corresponds to the number of dorsal scales. Unlike the dorsal scales, the dorsolateral scales do not overlap each other and there is no anterior spur.

The ventral scales are much smaller (<5 mm) than those of the other caudal series and are lozenge-shaped and imbricate, whereby each scale slightly overlaps the adjacent distal one (Fig. 4.7a, b). The scales progressively decrease in size distally and towards the ventral side of the tail, and it is unclear whether the ventral part of the tail was completely covered by scales. The ventralmost caudal scales are highly modified: their proximoventral edge extends as extremely elongated, bristle-like structures (up to four per scales, e.g., INREC K-4-4/5-28 and K-4-6d-34; Fig. 4.7c) that form dense and anteriorly oriented bundles (see INREC K4/9-41). In the latter specimen, the bristles are particularly thick (up to 1.5 mm wide) and long (>140 mm) (Fig. 4.6d). In smaller specimens and in the distal part of the tail, the bristles are much thinner (0.3 mm wide; Fig. 4.7c). Regardless of their size, these bristles typically exhibit multiple fractures along their length; this suggests that they were rigid (Fig. 4.6d). The unusual ventral position and anteroventral orientation of these bristle-like structures would have limited their role in protection.

Monofilaments Monofilaments are widely distributed around the head (Fig. 4.8a, b), thorax (Fig. 4.8c–e) and back. Their diameter is constant throughout their length. They do not show a hollow structure as they appear as cords, similar to hairs and individual barbs of downy feathers, and also to stage 1 in Xu et al.'s (2010) model for feather evolution. Whether the internal void space in hollow tubes, such as filament-like feathers in extant birds, can be retained during fossilization is, however, unknown. The monofilaments above the head are thin (ca. 0.15 mm wide), short (10–15 mm long), and curved, with no preferred orientation (Fig. 4.8b). The thoracic and abdominal filaments are wider (0.2–0.3 mm wide) and longer (20–30 mm). In INREC K4-6a-22, most of the monofilaments associated with the ribcage are consistently oriented craniocaudally within a 10°–15° interval (Fig. 4.8c–e). The typically curved geometry and continuous nature of these monofilaments indicates that they were likely flexible. The monofilaments in *Kulindadromeus* are thus shorter and thinner than those on the proximal part of the tail in *Psittacosaurus* (Mayr et al. 2002) and thinner than the filamentous structures in *Tianyulong* (Zheng et al. 2009).

Lingham-Soliar (2014) interpreted the monofilaments in *Kulindadromeus* as dermal collagen fibers or fiber bundles and not as epidermal structures, as it was also hypothesized for the thinner (<0.05 mm) monofilaments in the basal theropod *Sinosauropteryx* (Lingham-Soliar et al. 2007). Interpretations of the monofilaments in *Kulindadromeus* were based on comparative analysis with the thick bundles of collagen fibers present in the integument of marine tetrapods. The validity of a direct comparison between integumentary collagen in marine tetrapods and in a terrestrial dinosaur is, however, uncertain given the marked differences in mechanical stresses acting upon the skin in these animals. Indeed, Lingham-Soliar and Plodowski (2007) and Lingham-Soliar and Wesley-Smith (2008) showed previously that the organization of collagen fibers into thick bundles is linked to high tensile stiffness and efficiency of the locomotory organs in high-speed marine tetrapods.

Further, the morphology and arrangement of the fossilized filaments in *Kulindadromeus* is not consistent with that of *in vivo* or degraded collagen. *In vivo* integumentary collagen fibers typically occur in layered arrays of parallel, densely packed fibers where fibers in successive layers are oblique to one another. The filamentous structures in *Kulindadromeus* are straight to slightly curved, show constant width along their length, show a constant orientation, remain well separated from each other, and lack evidence for arrangement of fibers into successive vertical layers (Fig. 4.8). It is also difficult to envisage how the preserved arrangement of monofilaments could be generated during decay of collagen. Our ongoing experiments simulating the degradation of avian collagen reveal that the collagen fiber bundles of the dermal stratum compactum progressively dissociate and ultimately degrade into a dense tangled mass of highly anastomosing fibrils (Godefroit et al. 2014b).

Filaments Associated with a Basal Plate Importantly, *Kulindadromeus* shows compound, nonshafted integumentary structures, which can be directly associated with the proximal parts of the humerus (Fig. 4.9a–c) and femur (Fig. 4.9g–i). These occur as groups of six or seven filaments, each 10–40 mm long, that converge proximally and arise from the central, or even the basal region of a basal plate. This contrasts with the bristle-like structures that emerge from the edge of the lateroventral caudal scales (*contra* Saveliev and Alifanov 2014). Filaments on the humerus are thick (0.2–0.4 mm wide), straight and are extensively fractured (and therefore probably relatively rigid; Fig. 4.9b, c), whereas those on the femur are thinner (0.1–0.2 mm wide; Fig. 4.9d–f, h, i). The basal plates are larger on the humerus (3–4 mm wide; Fig. 4.9b, c) than on the femur (2–3 mm wide; Fig. 4.9e, f, h, i). On both the humerus and the femur, they show a hexagonal arrangement but

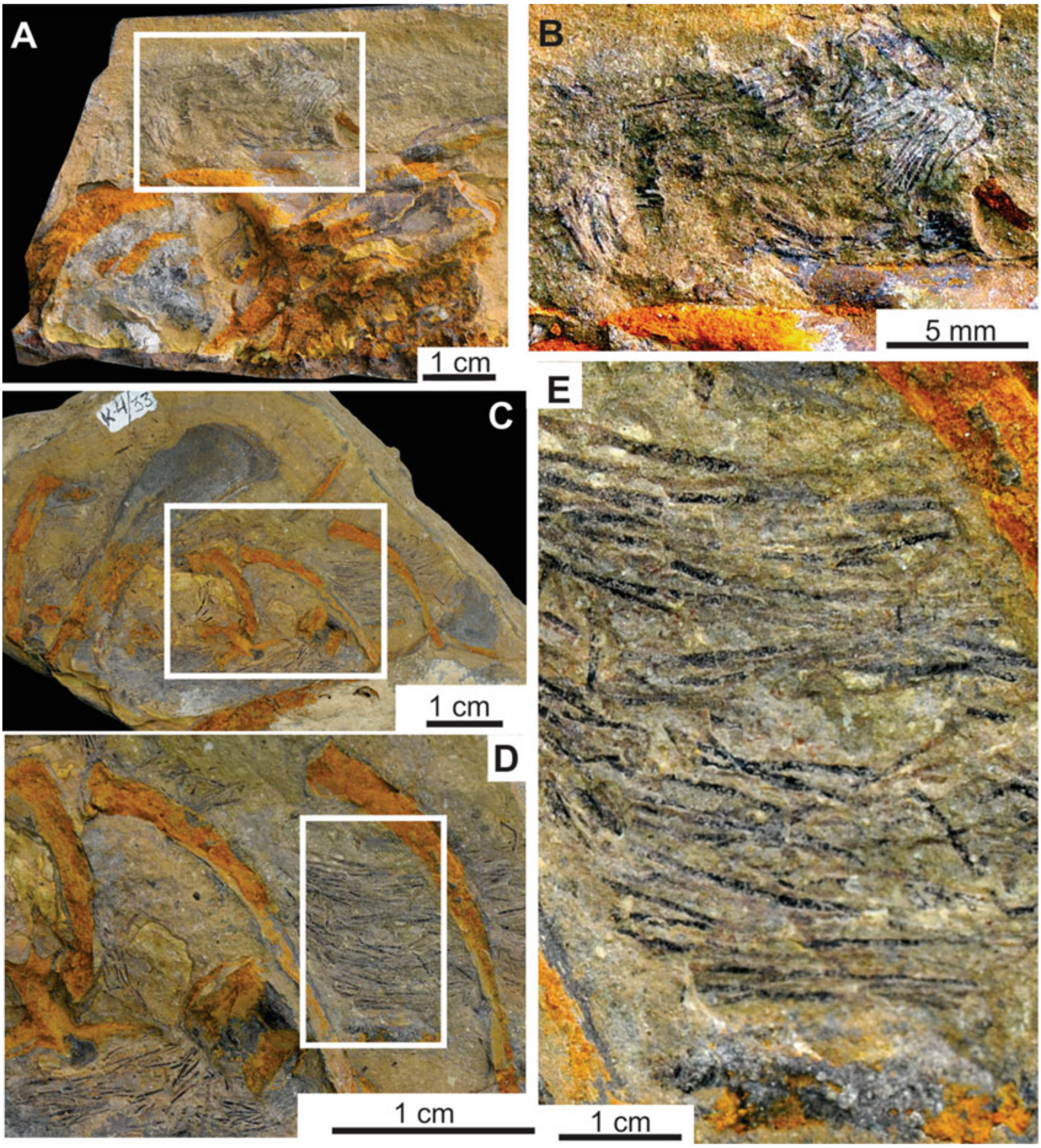

Fig. 4.8 Monofilaments in *Kulindadromeus zabaikalicus*. (**a**) partial skull (INREC K4/22) in right lateral view, with **b**, detail of areas indicated in (**a**); (**c**) left part of ribcage (INREC K4/33), with **d–e**, details of areas indicated in (**c**) and (**d**) showing filamentous structures

are mutually separated. This contrasts with the contiguous distribution of scales on the distal forelimb, hindlimb, and tail in *Kulindadromeus*, and also with that of the feathered scales that cover the tarsometatarsus of living birds (Lucas and Stettenheim 1972). Godefroit et al. (2014a) hypothesized that these groups of filaments are similar to the stage 2 feathers of Prum's (1999) and Xu's (2006b) model for feather evolution, in which the feather comprises a tuft of unbranched barbs joined proximally. This type of "protofeather" has been described in several feathered nonavian theropods or basalmost birds from northeastern China, including *Sinornithosaurus millenii* (Xu et al. 2001, fig. 3), *Microraptor gui* (Xu et al. 2003), *Anchiornis*

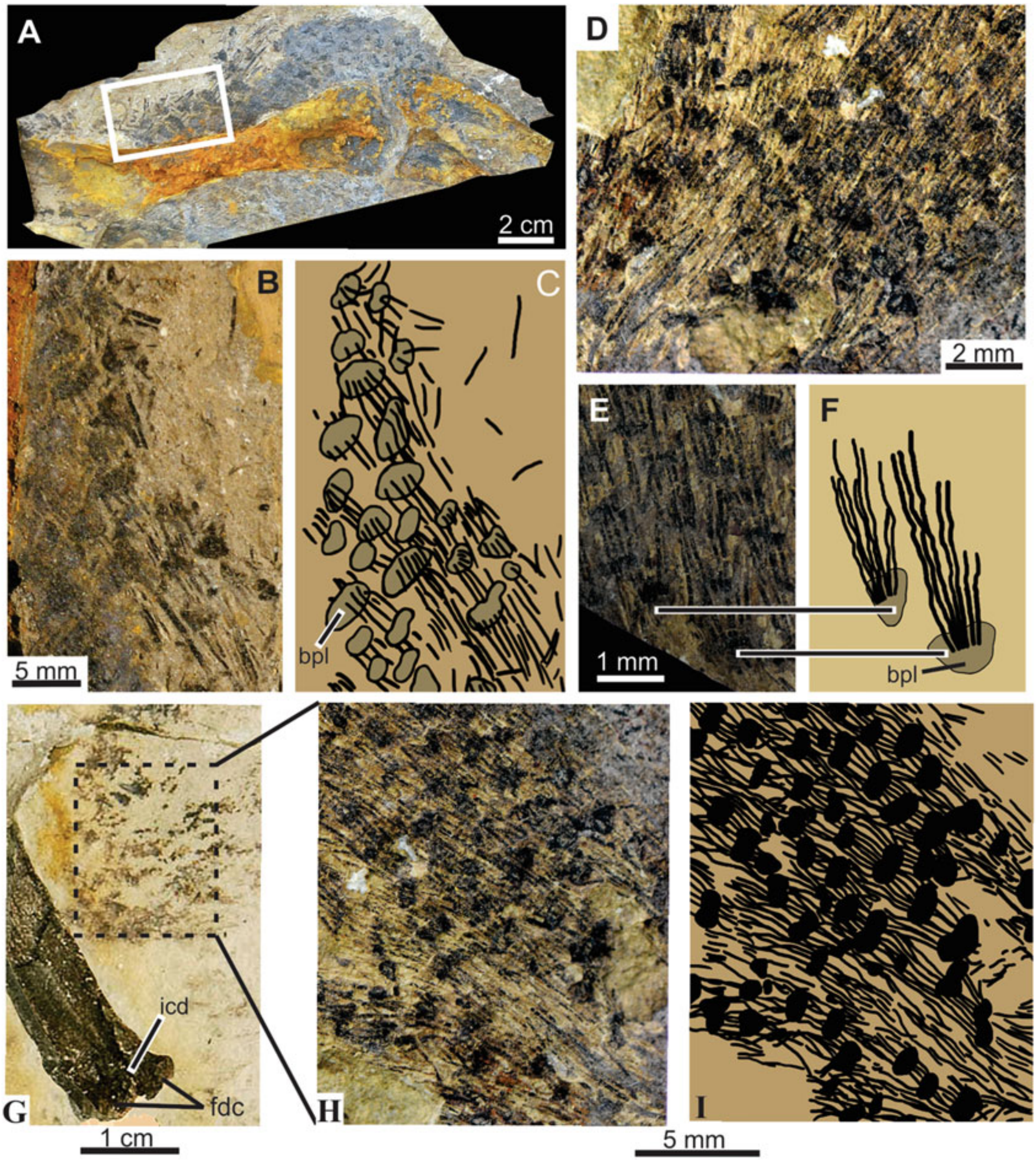

Fig. 4.9 Filaments associated with a basal plate in *Kulindadromeus zabaikalicus*. (**a**) Right humerus and proximal part of right radius and ulna (INREC K4/115), with detail (**b**) and interpretative drawing (**c**) of compound structures around the right humerus; (**d**) (INREC K4/88) and (**e**) (INREC K/117), compound structures, presumably around femur (part and counterpart of INREC K4/116) with, (**f**) interpretative drawing of (**e**); (**g**) distal part of right femur; (**h**) detail of the counterpart of INREC K4/116 showing compound structures; (**i**) interpretative drawing of (**h**). *bpl* basal plate, *fdc* femoral distal condyles, *icd* intercondylar groove

huxleyi (Hu et al. 2009, fig. 3h), *Eosinopteryx brevipenna* (Godefroit et al. 2013, fig. 2i), and *Similicaudipteryx yixianensis* (Xu et al., 2010), and was also likely present, according to Xu and Guo, in *Beipiaosaurus inexpectus*. Filamentous parallel barbs arising from the edge of a membranous structure also occur in *Epidexipteryx hui* (Zhang et al. 2008, fig. 2d, e).

According to Prum (1999), stage 2 plumulaceous feathers are radially symmetrical. Because the stage 2-like structures in *Kulindadromeus* and feathered nonavian theropods from Liaoning are preserved as discrete, two-dimensional outlines, whether those structures were already planar *in vivo*, or were originally circular and subsequently compressed during fossilization remains unclear. The basal plates in *Kulindadromeus* unlikely correspond to feathered scales, as observed in domestic pigeons, chickens, and barn owls, because they are not contiguous or overlapping. In *Kulindadromeus*, the distal filaments of those compound structures are usually slightly divergent and did not overlap each other during fossilization; this is consistent with the arrangement of similar groups of filaments in nonavian feathered theropods, but not with diagenetic compression of filaments arranged in a circular fashion, which would have resulted in overlapping filaments. The recurrent geometry of the filaments in the fossil compound structures suggests that the structures originally were arranged in a planar fashion *in vivo*.

An alternative interpretation of the fossil compound structures is offered by Lingham-Soliar (2014), in which the compound structures around the humerus and femur are interpreted as collagen support fibers associated with badly degraded scales. Godefroit et al. (2014b) considered this hypothesis highly unlikely due to the taphonomy and morphology of the preserved structures. An analysis of more than 1000 isolated bones and partial skeletons has revealed that different integumentary structures are systematically associated with specific anatomical regions: small nonoverlapping scales occur in the distal hindlimb (distal tibia + pes) and the manus; larger imbricated scales occur above the tail; long bristle-like structures emerge from the ventrodistal edge of small overlapping scales along the ventrolateral side of the tail; monofilaments occur in the head and the thorax, grouped filaments, and basal plate; in the proximal parts of the limbs (humerus and femur); and clusters of ribbon-shaped elements occur around the proximal tibia (see below). If the basal plates represent badly degraded scales (Lingham-Soliar (2014), it is difficult to envisage a scenario in which scales were selectively degraded and/or disarticulated around the humerus and femur, but never around the distal tibia, pes, and tail. The different anatomy and mode of preservation of the structures preserved in the tail and distal parts of the limbs, and those preserved in the rest of the body, support our interpretation that the two sets of features represent fundamentally different structures—the fossilized remains of epidermal scales and "protofeather"-like structures, respectively. The suggestion that collagen fibers or fiber bundles would be better preserved than scales (Lingham-Soliar 2014), is inconsistent with previous studies demonstrating that keratin has a higher preservation potential than collagen (Bjelland et al. 1988; Davis and Briggs 1995; Brown and Brown 2011). Our own decay experiments using feathers reveal that these are much more robust than the collagenous dermis and retain gross morphological characteristics for a longer period during decay (Godefroit et al. 2014b). The excellent state of preservation of the filaments in *Kulindadromeus* thus supports our interpretation that they represent keratinous structures rather than collagen fibers or fiber bundles.

Ribbon-Shaped Structures Ribbon-shaped structures associated proximally into clusters of six to seven elements occur along the proximal part of the tibia (Fig. 4.10). Each individual element is 15–20 mm long and 1.5–3 mm wide with a dark axial lineation (Fig. 4.10b–d). A thin superficial carbonaceous sheet envelops ca. 10 thin internal (50–100 μm) parallel filaments (Fig. 4.10d).

Similar broad (2–3 mm) monofilaments have been reported in the basal therizinosaur *Beipiosaurus inexpectus*, from the Early Cretaceous Yixian Formation of Liaoning Province, China (Xu et al. 2009), but are much longer (about 100–150 mm) than those in *Kulindadromeus* and not bundled proximally. Tail feathers with a ribbon-like proximal portion and a pennaceous distal tip have been described in a juvenile specimen of the oviraptorosaur *Similicaudipteryx yixianensis* (Xu et al. 2010), and also in the basal maniraptoran *Epidexipteryx*

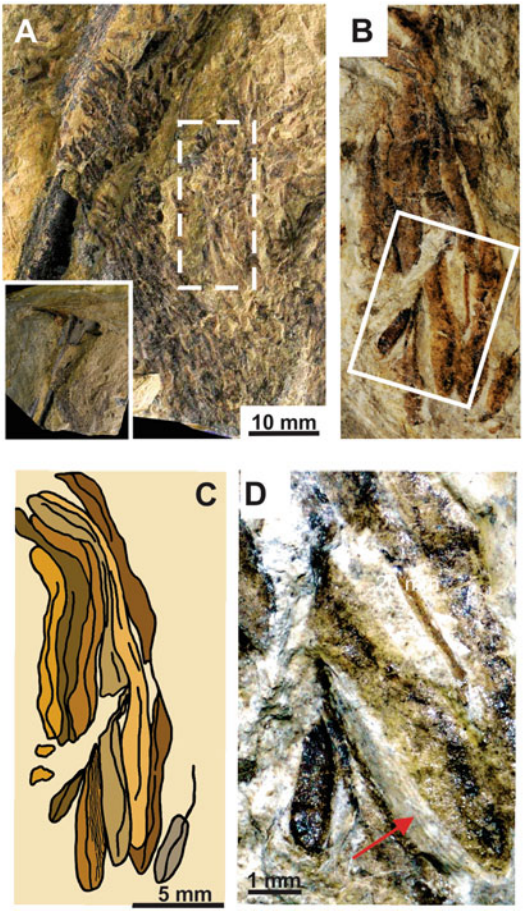

Fig. 4.10 (**a**) Ribbon-like structures around proximal part of tibia (INREC K4/44); inset shows slab in lower magnification; (**b**) detail of area indicated in **a** with interpretative drawing (**c**) and further details of ribbon-like structures (**d**); the superficial carbonaceous sheet has been removed during preparation, revealing an internal structure of thin parallel filaments (arrow)

hui (Zhang et al. 2008; Xu et al. 2010). Prum (2010) and Foth (2012) observed that juvenile tail feathers of *Similicaudipteryx* closely resemble the morphology of molting feathers of living birds and that those proximally ribbon-like pennaceous feathers could represent "pin feathers" or developing feather germs. The tubular feather germ is surrounded by a keratinized sheath that is lost during development to expose the mature feather. Typically, the sheath begins to dissociate from the mature distal tip of the feather before the ensheathed tubular base of the feather is fully developed. For a pennaceous feather, this intermediate stage of growth appears as a limited distal vane emerging from a smooth tubular base, corresponding to the morphotype observed in the juvenile *Similicaudipteryx* (Prum 2010).

Lingham-Soliar (2014) stated that ribbon-like structures, similar to those described in *Kulindadromeus*, occur as structural collagen in blood vessels, the *linea alba* (which separates the central band of abdominal muscles), and the rectus sheath. Godefroit et al. (2014b) noted that the arrangement, size, and morphology of the ribbon-like structures is strongly dissimilar to that of a network of circulatory vessels, which typically shows frequent branching and a reduction in diameter distally. Secondly, thick bands of connective tissue in the *linea alba* and rectus sheath occur in the human body where large muscles connect either to each other or to bone. It is highly unlikely that *Kulindadromeus* possessed similar, particularly large muscles in the region of the tibia and thus it is unlikely that the ribbon-like structures represent structural collagen (Godefroit et al. 2014b).

4.5 Discussion

The presence of both simple and compound filamentous structures in *Kulindadromeus* supports previous reports of simple "protofeather"-like structures in the ornithischian dinosaurs *Psittacosaurus* (Mayr et al. 2002, 2016) and *Tianyulong* (Zheng et al. 2009; Sereno 2012). Critically, this discovery confirms that monofilaments (i.e., stage 1 of Xu et al. 2010) and grouped filaments arising from a basal plate (similar to stage 2 of Prum 1999, and stage 3 of Xu et al. 2010) were not a synapomorphy of coelurosaurian theropods but were also present, and could form extensive body coverings, in ornithischians. Given the phylogenetic position of these taxa near the evolutionary base of ornithischians, these findings imply that the common ancestor of theropods and ornithischians also possessed simple feather structures. Regardless of the adopted phylogenetic hypothesis (Baron 2017), this common ancestor lived during the Upper Triassic. Scaly, nonfeathered, skin has been described in several groups on both the ornithischian and theropods branches of the dinosaur family tree (Witmer 2009; Barrett et al. 2015), which suggests that protofeathers were probably lost several times in dinosaur evolution. Furthermore, the ability to form monofilaments and more complex compound epidermal structures is potentially nested within the archosauromorph clade, as exemplified by *Longisquama* (Buchwitz and Voigt 2012) and pterosaurs (Bakhurina and Unwin 1995; Wang et al. 2002; Yang et al. 2019). The ultimate question of whether these monofilaments and compound filaments of primitive ornithischians represent part of the evolutionary lineage of feathers in paravian dinosaurs or, as hypothesized by Barrett et al. (2015), independent evolution of projecting epidermal appendages, remains unclear. Monofilaments, as the first step towards the development of "true" feathers, are similar to hair shafts, the other great category of filamentous epidermal structures in tetrapods. Contrasting with feathers, the geometry and anatomy of hairs has not changed during mammal evolution, as it was already present more than 160 million years ago, in Middle-Late Jurassic basal mammaliaformes (e.g., Ji et al. 2006). The important point is that the flight feather vane in living birds is the most complex epidermal appendage known in modern and ancient animals. One of the main reasons why hairs have never evolved branched structures might be the shape of their collar: pointed in hairs and ring shaped in feathers (Prum and Brush 2002). Current data is insufficient to dismiss the hypothesis that other complex integumentary structures, different to the feather vane, might have independently evolved in nonavian archosauromorphs.

As in living birds, *Kulindadromeus* confirms other evidence that scales and "protofeather"-like structures are not mutually exclusive in a single dinosaur taxon. Small, tubercle-like scales are known from the limb and tail of a psittacosaur that bears bristle-like structures above its tail (Mayr et al. 2002, 2016; Vinther et al. 2016). Patches of scaly structures have been reported from the tail and tibiae in the compsognathid theropod *Juravenator starki*, from the Late Jurassic of Bavaria, Germany (Göhlich and Chiappe 2006). Given that the "scaly" *Juravenator* is closely related to the "fuzzy" *Sinosauropteryx*, Göhlich and Chiappe (2006) hypothesized that the early evolution of feather structures may have been flexible and experimental (see also Xu 2006a, b). Per Xu (2006a), the presence of protofeathers in *Sinosauropteryx* and their absence in *Juravenator* might also be explained by slight differences in the phylogenetic position of those coelurosaurians, *Juravenator* being slightly more primitive. However, the latter hypothesis was subsequently invalidated by the discovery of protofeathers in the more basal megalosauroid *Sciurumimus albersdoeferi*, also from the Late Jurassic of Bavaria (Rauhut et al. 2012). The coexistence of "protofeather"-like structures and scales in *Kulindadromeus* suggests the potential for the body of *Juravenator* to have had a similar "fuzzy" covering of monofilaments that are not preserved.

The diversity and localized distribution of specific integumentary structures over the body of *Kulindadromeus* indicate that the various integumentary structures had different functional adaptations. The simple filaments around the head, thorax, and back may have functioned in insulation, but it is difficult to assess whether their density was sufficient to form an effective insulating layer. The compound filaments associated with a basal plate and the ribbon-like structures occur in the proximal parts of the limbs, and therefore probably did not function primarily in insulation. The regular organization of the basal plates and the clustered arrangement of the ribbon-like structures suggests that they may have functioned in visual display. It is also possible that these integumentary structures had ancillary functions in balance or insulation of eggs. The scales around the tail and the bristle-like structures on the lateroventral aspect of the tail were obviously too thin for efficient defensive functions but rather likely stiffened the tail dorsoventrally, the latter acting as a pendulum.

4.6 Conclusions

The body of *Kulindadromeus zabaikalicus* was covered by diverse integumentary structures, including different types of scales and filaments

Fig. 4.11 Tentative reconstruction of *Kulindadromeus zabaikalicus*, showing the distribution of the various integumentary structures. Model by Mostfa Mohammed

(Fig. 4.11). The different structures are systematically associated with specific anatomical regions: (1) small nonoverlapping scales are localized to the distal hindlimb (distal tibia + pes) and the manus, (2) larger imbricated scales with a proximal spur, to dorsal regions of the tail, (3) smaller imbricated scales with associated bristle-like structures, to the lateroventral region of the tail, (4) monofilaments, to the head and thorax, (5) clusters of filaments that diverge from a basal plate, to the proximal parts of the limbs (humerus and femur), and (6) clusters of ribbon-shaped structures, to the proximal tibia. All of these structures are most likely epidermal in origin (*contra* Lingham-Soliar 2014). Ongoing analyses of the ultrastructure and chemistry of the different integumentary structures in *Kulindadromeus* will provide a deeper understanding of the anatomical affinity of these structures and, in turn, of the origin and early diversification of epidermal structures, including feathers, in Archosauromorpha. The insights yielded by these ultrastructural and chemical studies will be complemented by our further sedimentological, mineralogical, and taphonomic studies of the Kulinda locality in order to better understand the environmental and diagenetic circumstances leading to exceptional preservation of integumentary features in *Kulindadromeus*.

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