The story of how feathers evolved is far from over.

THE FUZZY FRONTIER

BY STEVE SALISBURY

ILLUSTRATION BY JAMES REECE

(Previous page) ***Confuciusornis*** **is one of the oldest birds known after *Archaeopteryx*. Literally hundreds of specimens of this magpie-sized bird have now been found in Liaoning Province, suggesting it may have lived in large colonies around the forested lake margins. It is much more bird-like than *Archaeopteryx*, with a considerably larger breastbone, reduced bony tail and no teeth. *Confuciusornis* was apparently sexually dimorphic, with many of the larger specimens—presumably the males—possessing a pair of exceptionally long, scale-like tail feathers.**

In 1868, Thomas Huxley declared that dinosaurs gave rise to birds. He based his claim on *Compsognathus*, a 150-million-year-old dinosaur fossil from Solnhofen, Germany, whose delicate hind legs were remarkably similar to those of table fowl. The discovery seven years earlier of *Archaeopteryx*, a fossil bird with a long bony tail, toothed jaws and clawed fingers, had convinced many people that birds were somehow related to reptiles. But *Compsognathus* was the fossil that placed dinosaurs firmly in the middle of this complex evolutionary equation. Wings, claimed Huxley, must have grown out of rudimentary forelimbs. And feathers? Whether *Compsognathus* had them, Huxley could only guess. Nevertheless, his theory clearly required that scales had somehow transformed into feathers. The question was not just how, but why?

LIAONING PROVINCE *seemed to be transforming theropods into a motley crew of fuzzy feathered freaks overnight.*

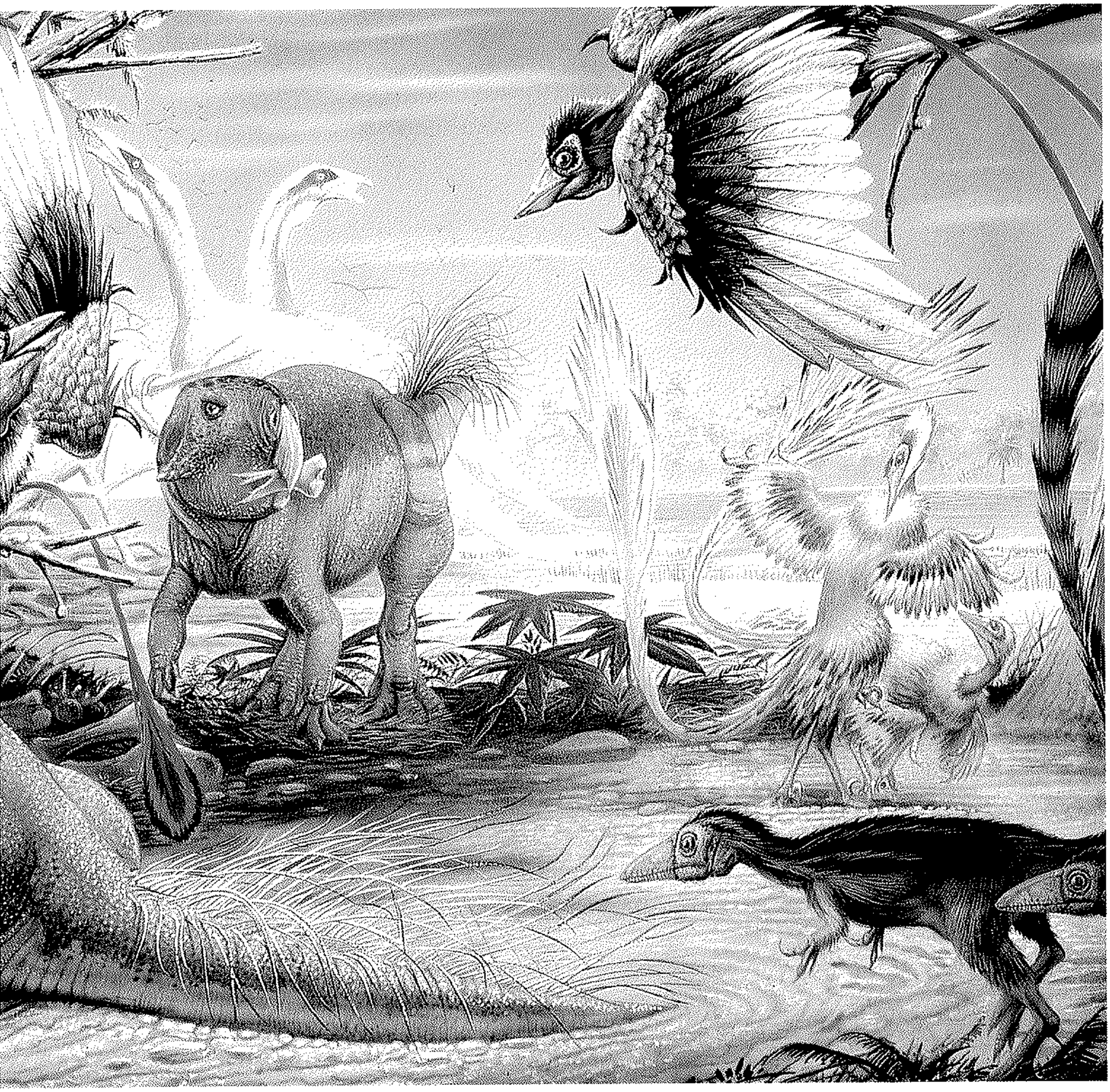
In October 1996, Chinese and Canadian palaeontologists revealed sensational photographs of a new theropod dinosaur from China. The scientific world stood with its jaws agape. This was *Sinosauropteryx* ('Chinese dragon feather'). About a metre long, the 125-million-year-old fossils from Liaoning Province, north of Beijing, looked very similar to those of *Compsognathus*, except for one, very striking difference: each *Sinosauropteryx* specimen was surrounded by a halo of dark, fuzzy fibres (see "Feathered Dinosaur", *Nature Aust.* Spring 1997).

As news of these dinosaurs spread, palaeontologists began arguing over what the strange fibres represented. To many, the best explanation was that they were long filamentous integuments, not unlike mammalian hair, only much thicker. As such, they could be considered proto-feathers, the long-sort-after transitional structure between elongate reptilian scales and simple down-like feathers. Others, however, were quick to dismiss these fibres as frayed bits of decaying flesh, most likely collagen, a protein found in connective tissue. But before any kind of consensus could be reached, Liaoning produced another two, even more amazing fossils: *Protoarchaeopteryx* and *Caudipteryx*.

While there may have been doubts about the body covering of *Sinosauropteryx*, this wasn't the case with *Protoarchaeopteryx* and *Caudipteryx*. Both these dinosaurs were covered in structures that clearly resembled bird feathers. So much so, in fact, that many critics of the theropod–bird link believe they aren't dinosaurs at all, but belong to a group of archaic flightless birds.

Protoarchaeopteryx and *Caudipteryx* are each about the size of a turkey, but with much longer legs and a bony tail. *Protoarchaeopteryx* has both contour and down-like feathers on its body and a bizarre, fan-like arrangement of larger, 'true' feathers sprouting from the end of its tail. The tail fan is even more pronounced on *Caudipteryx*, hence its name, which means 'tail feather'. *Caudipteryx* also has a tuft of 'true' feathers attached to its second, clawed finger.

In palaeontology it's usually a long wait between major discoveries. In the case of feathers and fuzz, for example, we had to wait 135 years between the first *Archaeopteryx* specimen and *Sinosauropteryx*. In the late 1990s, however, Liaoning Province seemed to be transforming theropods into a motley crew of fuzzy feathered freaks overnight. In 1999, hot on the heels of *Protoarchaeopteryx* and *Caudipteryx* came

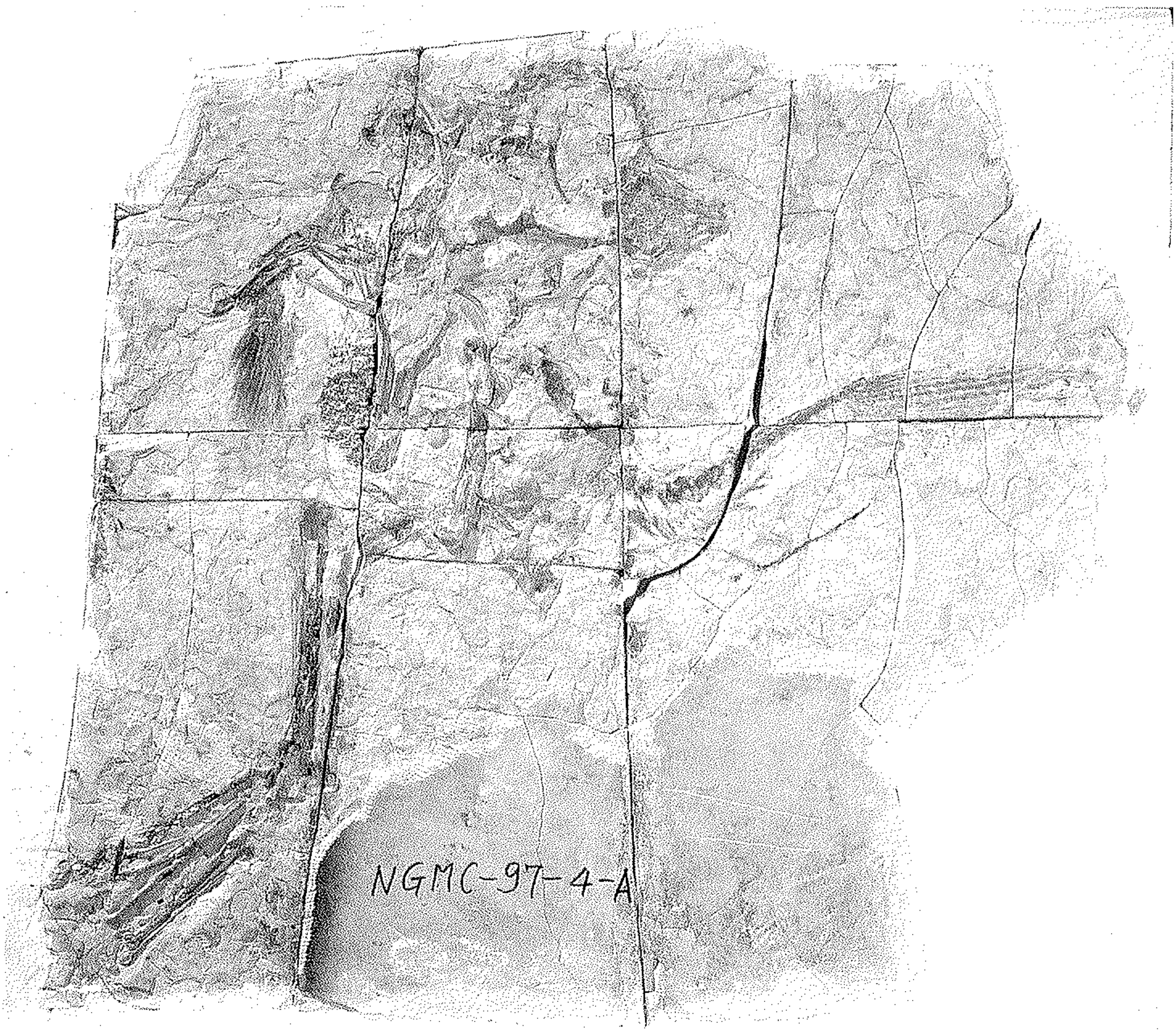


LUIS V. REY

Beipiaosaurus. Estimated to have been over two metres long, *Beipiaosaurus* is the largest fuzzy dinosaur yet found. It is also one of only a few dinosaurs that belong to Therizinosauridae, an unusual group of theropods endemic to eastern Asia and North America. The discovery of feather-like filaments in a therizinosaurid signalled to palaeontologists that fuzz may have been much more ubiquitous among theropods than was initially thought.

And they were right. A few months later, Liaoning turned up the 'Chinese bird dragon' *Sinornithosaurus*, the theropod everyone had been waiting for. This is because it is a 'feathered' dromaeosaurid, or 'raptor' (see "Dinosaurs of a Feather...", *Nature Aust.* Spring 2000), and of all the dinosaurs, it is the dromaeosaurids that are most similar to birds anatomically. At first glance, the turkey-sized *Sinornithosaurus* looks like it was covered in shaggy black hair. However, detailed analysis of these structures has revealed that they are in fact multiple branching filaments, as opposed to the simple, fibre-like struc-

A reconstructed scene from the heart of the fuzzy frontier—Liaoning Province, north-eastern China, 125 million years ago. In the right foreground, two 'proto-feathered' *Sinosauropteryx* approach a pair of *Psittacosaurus*, a beaked ceratopsian dinosaur with quill-like structures along the upper surface of its tail. Behind them, two *Beipiaosaurus* browse the lower branches of lakeside trees for insects. At two metres in length these unusual-looking therizinosaurids were the largest of the fuzzy dinosaurs of their day. To the right of the *Psittacosaurus*, feathered dromaeosaurids ('raptors') display to each other to assert dominance. Two male *Confuciusornis*, one of the world's first flying birds, play out a similar game in the trees.



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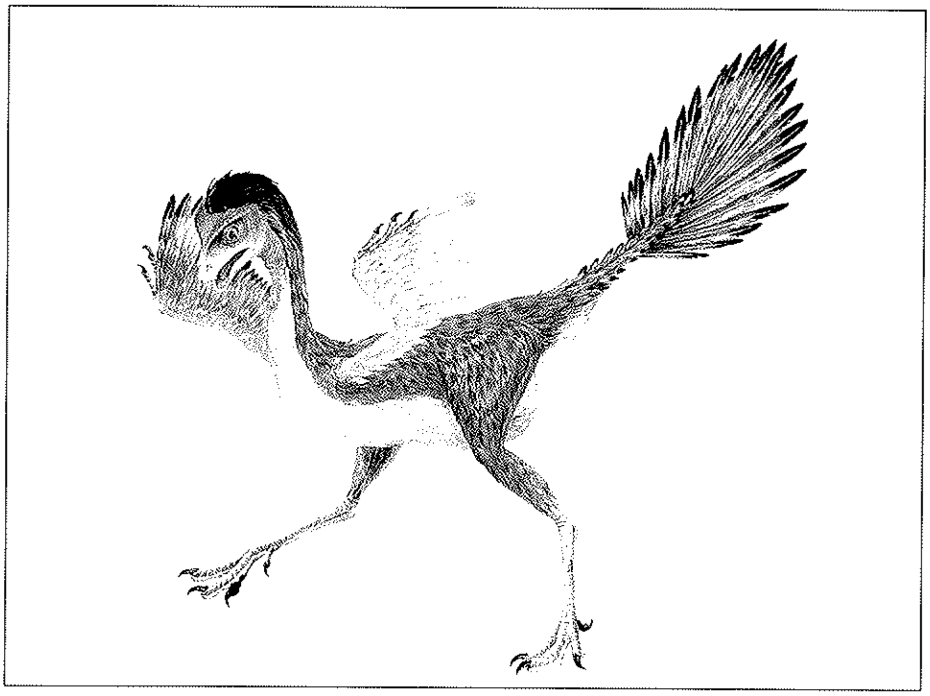

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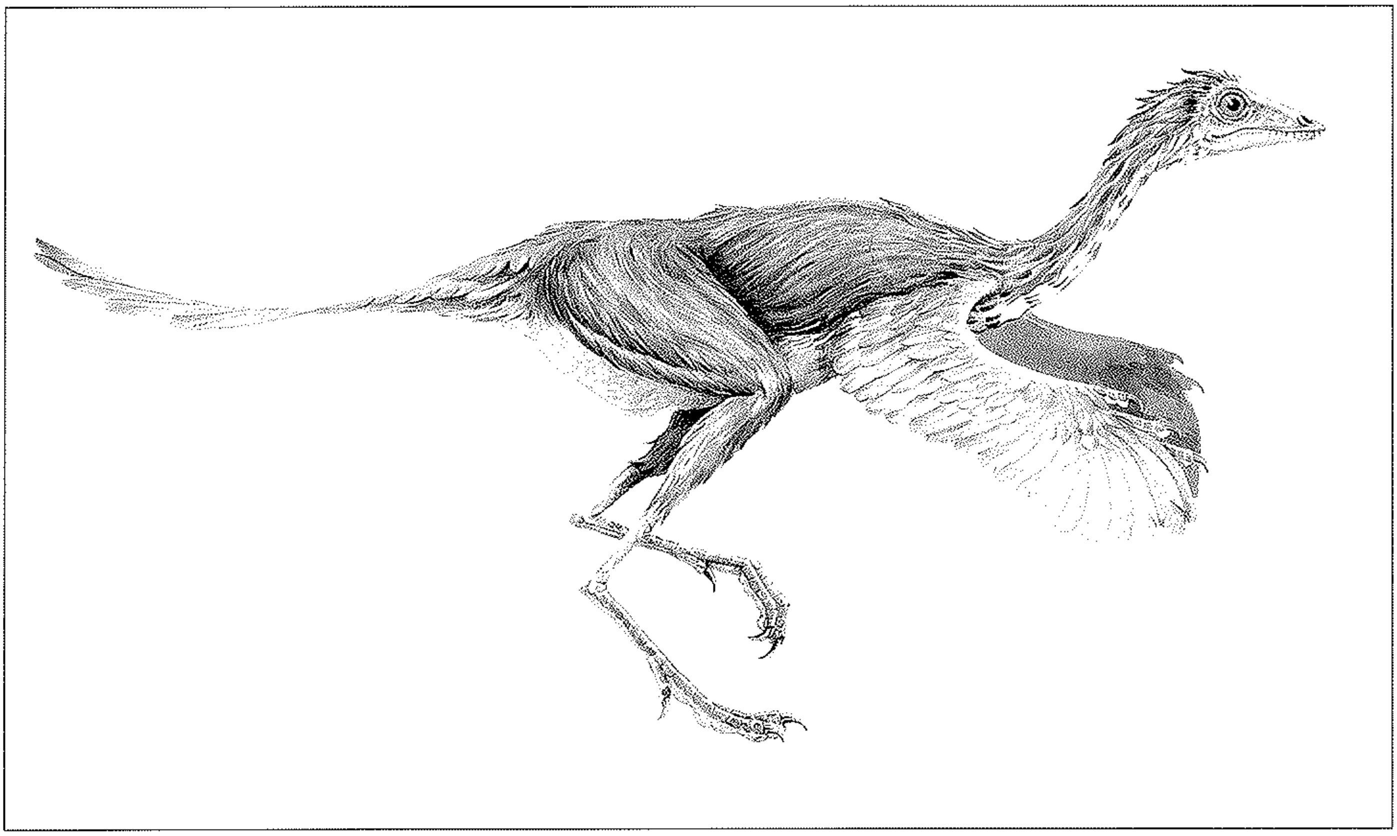
The turkey-sized *Caudipteryx* (left) must rank as one of the most unusual dinosaurs ever discovered. Articulated skeletons (above) of several individuals have now been found in Liaoning Province, north-eastern China. Attached to each of its short, clawed forelimbs was a tuft of long, symmetrical feathers. In combination with the jaunty fan of feathers sprouting from the tip of its tail, they may have been used for threat and mating displays in a manner similar to many modern-day ground birds.

tures adorning *Sinosauropteryx* and *Beipiaosaurus*.

Both fuzzy and feathered theropods continue to be discovered. The flock now includes four more dromaeosaurids: two species of *Microraptor* and another two that are yet to be named, including one that is clothed in feathers almost identical to the down feathers of modern birds. Amazingly,



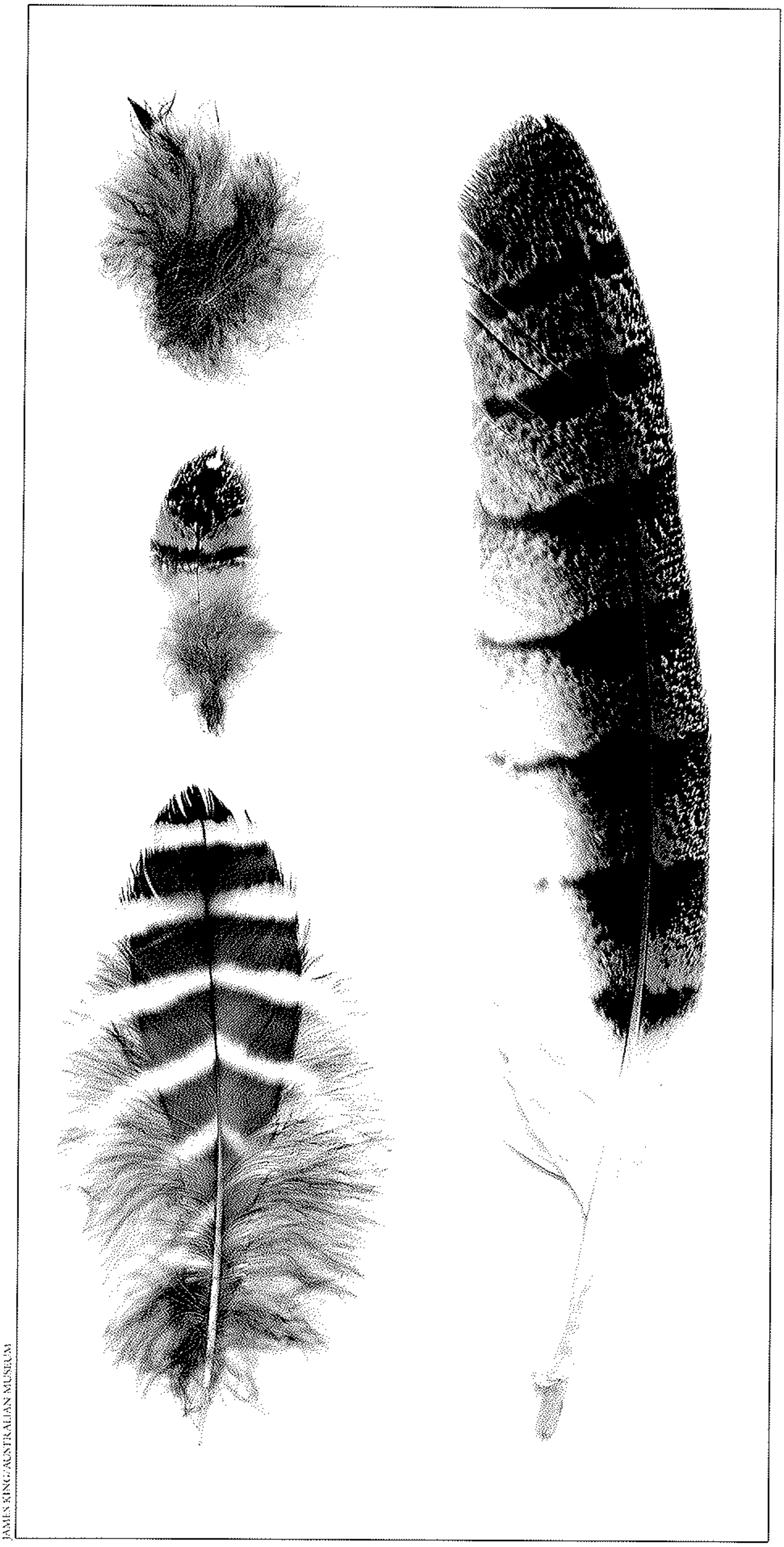
***Protoarchaeopteryx* is known from a single, frustratingly incomplete fossil that was first unveiled in 1996. About the same size as *Caudipteryx*, it also had a clump of symmetrical feathers attached to the end of its tail. Its arms, however, were much longer, with huge, sharply clawed hands that would have been ideal for seizing small prey, and its hind limbs suggest it was a fast and efficient runner.**

one of the newly described *Microraptor* species sports four wings; both its fore- and hind limbs, as well as the tail, are adorned in fully modern, asymmetrical feathers (see box). And it's a safe bet that, by the time this article is published, more will have been unearthed.

PRIOR TO THE DISCOVERY OF *Sinosauropteryx*, most hypotheses for the evolution of feathers have involved flying. Scales were thought to have become more elongate in order to increase the surface area of the body without adding additional weight. The only problem with this is that, except for the four-winged *Microraptor*, which appears to have been a glider, none of the recently discovered fuzzy or feathered theropods from China was apparently able to fly. The feathers on the 'wings' and tail of *Caudipteryx*, the most bird-like (at least in terms of the arrangement of its feathers) of any of these new Chinese dinosaurs, are symmetrical. This characteristic, coupled with *Caudipteryx*'s proportionately long legs and short arms, suggests it was about as airworthy as an Emu. If we accept that the integumentary structures on dinosaurs such as *Sinosauropteryx* and *Caudipteryx* are the precursors to feathers, then we must also accept the idea that feathers did not originally evolve for flight. So why did they evolve?

AS MANY *palaeontologists have pointed out, if these dinosaurs could not fly, then why did they evolve such complex feathers?*

For many palaeontologists, the discovery of fossil fuzz adds weight to the idea that some dinosaurs were warm-blooded. For a warm-blooded theropod, proto-feathers would have conserved heat and protected the body from external temperature fluctuations. Flight feathers, therefore, must have come later. But the presence of essentially modern feathers on the wings and tail of both *Protoarchaeopteryx* and *Caudipteryx* is not entirely consistent with this idea. As many palaeontologists have pointed out, if these dinosaurs could not fly, then why did they evolve such complex feathers? Hair-like structures are much simpler and more efficient for thermoregulation. Furthermore, just because modern birds are warm-blooded and have feathers does not mean that this was also the case with early birds and fuzzy theropods. Warm-bloodedness is energetically expensive and requires a complex physiology (see "Crocodiles and Dinosaurs", *Nature Aust.* Summer 2000–2001). While it is by no means dependent on an insulatory body covering, warm-bloodedness does require a highly effective respiratory system. To date, interpreting the physiology of fuzzy dinosaurs and early birds based purely on osteological (bone) and even integumentary evidence is extremely difficult, and a con-



Down (top left), contour or body (middle left) and flight (right) feathers of a Masked Owl (*Tyto novaehollandiae*), and a contour feather (bottom left) of a Powerful Owl (*Ninox strenua*).

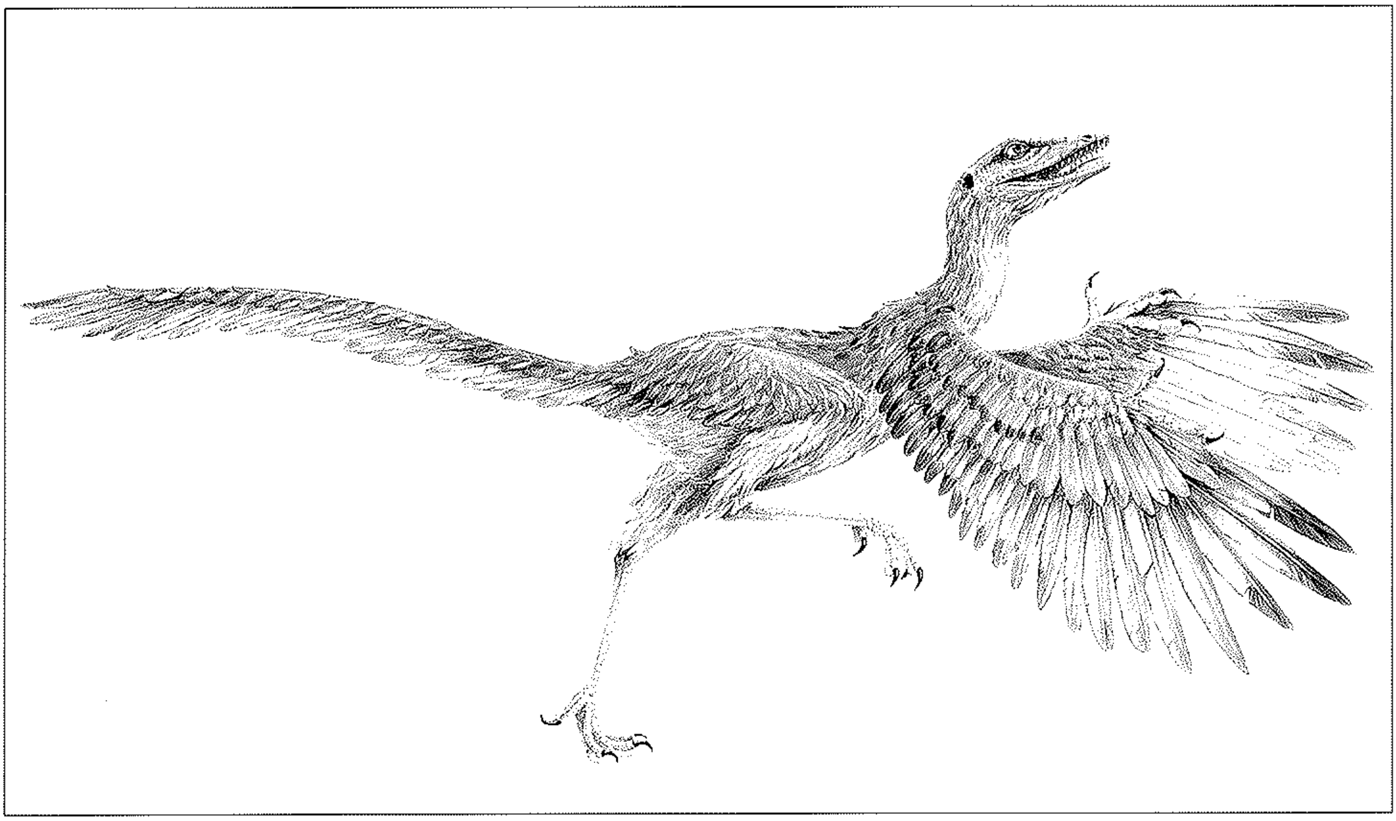
FEATHER FACTS

Like hair or scales, feathers are formed from the outer layer of skin and are made of a substance called keratin. Contour (body) and flight feathers have a hollow central shaft (the quill) that divides the feather into two vanes, each of which comprises a series of barbs. Adjacent barbs are hooked together by tiny structures called barbules. Consequently, each vane acts as a single interlocking sheet rather than a series of separate hairs. Contour feathers only have barbules on the barbs towards the tip. The barbs at the base are therefore separate, and often take on a ruffled, almost hair-like appearance. Barbs on down feathers lack barbules altogether. Some down feathers even lack a quill.

The feathers of modern birds come in many shapes and sizes, each type serving multiple purposes. For instance, primary and tail feathers are used for flight and display, whereas down feathers help maintain body heat.

A bird's flight feathers are anchored tightly to its wing bones. The primary flight feathers are attached to the wrist and hand, forming the outer half of the wing, whereas the secondary flight feathers are attached to the forearm. A small tuft of secondaries, known as the alula, is also attached to remnants of the thumb.

If a bird's secondaries are clipped, it can still fly, but remove no more than the tips of its primaries and it will be grounded. The reasons for this seem to relate to the shape of each type of feather, specifically its vanes. The primaries of flying birds have asymmetrical vanes. The leading edge is thinner than the trailing edge, so that each feather has an airfoil-like cross-section. With the wing fully spread, it is thought that the outer half of each primary acts as a small, independent airfoil or winglet, helping to increase the lift generated by the rest of the wing during takeoff and to prevent stalling at low flying speeds. If these winglets are taken out of the equation, the total amount of lift generated by the wing is reduced considerably, making flapping flight almost impossible to maintain. In flightless birds, however, the vanes on the feathers that are attached to the wrist and hand are symmetrical, similar to the secondaries of flying birds. Lacking an aerodynamic profile, these symmetrical feathers do not generate very much lift when the wing is extended and flapped. Combined with the smaller size of their wings, this is probably one of the main reasons why birds with fully symmetrical wing feathers can't fly.



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Still considered the world's oldest bird, *Archaeopteryx* was first discovered in 1859 in the lithographic limestones of Solnhofen, southern Germany. It is similar to many theropod dinosaurs in possessing a toothed beak, claws on its fingers and a long, bony tail. Its wings, on the other hand, are very avian, with the same number of primary and secondary flight feathers as those of modern-day flying birds. Although incapable of sustained flapping flight (as indicated by its small wishbone), *Archaeopteryx* probably partook in rudimentary aerial excursions, if only for short distances.

sensus among palaeontologists is a long way off.

In light of the shortcomings associated with both the flight and insulation hypotheses, many palaeontologists have opted for a slightly 'sexier' idea, suggesting that the symmetrical feathers of *Protoarchaeopteryx* and *Caudipteryx* evolved for use in mating and threat displays. Another idea for the origin of feathers relates to biomechanical support. It's now known that feathers and feather-like structures in the skin can help brace the body against mechanical loads such as torque during fast running. Lacking the fused skeletal elements seen in modern birds, particularly the speedy ratites, some theropods may have evolved proto-feathers in order to 'tighten up' their running style. The same principle was used by Nike to develop the body-hugging suit that helped Cathy Freeman win gold in the 2000 Olympics.

FEATHERS AND *feather-like structures in the skin can help brace the body against mechanical loads during fast running.*

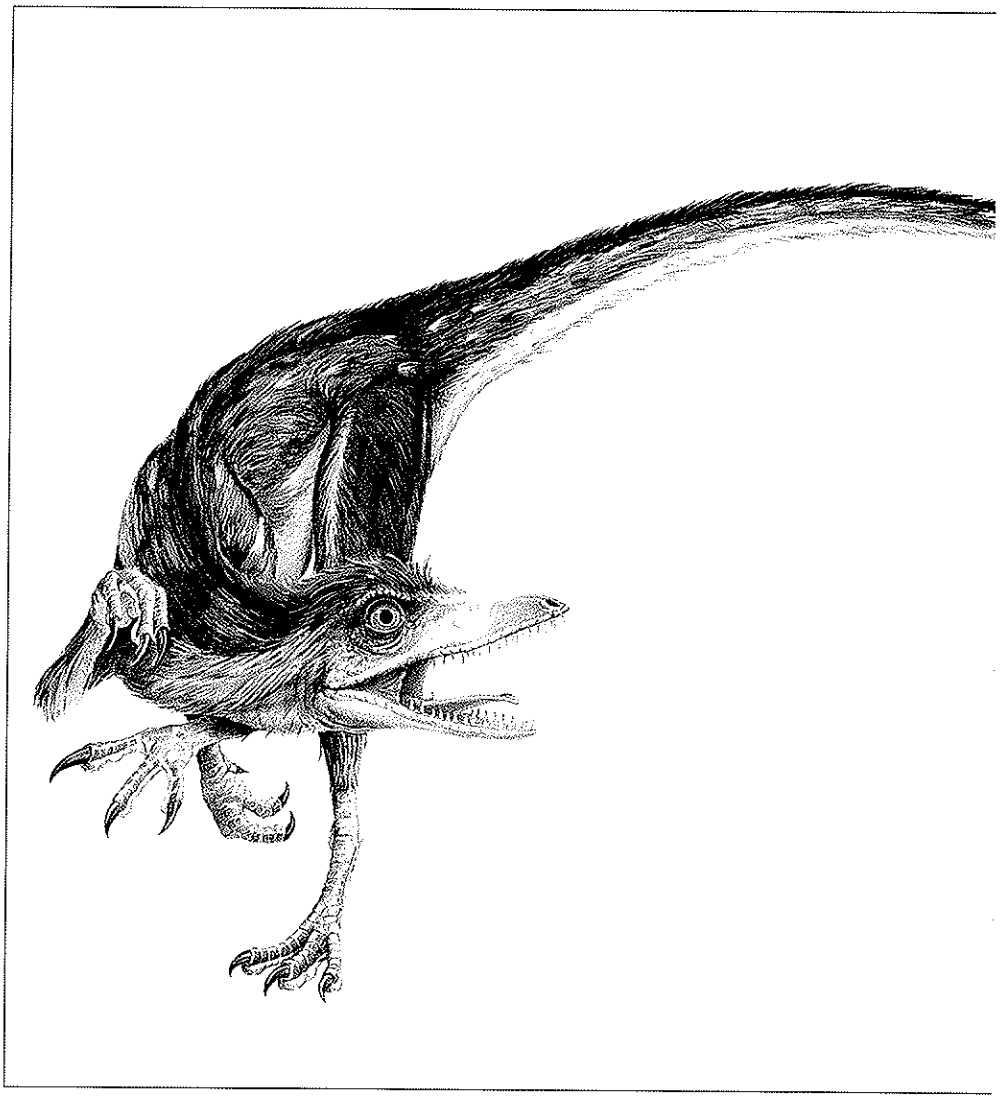
DESPITE THE RECENT FLURRY OF fuzzy fossil finds and new evolutionary scenarios for the origin of birds, the story of how feathers evolved is far from over, and a number of fossils are causing palaeontologists to rethink their ideas. One such fossil is *Longisquama*. This 220-million-year-old, mouse-size reptile from Kyrgyzstan, central Asia, had received little attention since it was first described in 1970. But after seeing the specimen in 1999, Terry Jones (Oregon State University) and colleagues decided it was far more bird-like than previously thought. What got their attention was *Longisquama*'s 'plumage': sprouting from the midline of its back is a series of paired, vane-like integumentary appendages up to 12 centimetres long.

When it was first discovered, *Longisquama*'s integumentary appendages were considered to be elongate scales, possibly used for gliding or sexual display. But Jones *et al.* interpreted them as feathers, thrusting *Longisquama* from relative obscurity into the centre of a bitter evolutionary debate. For not only does *Longisquama* pre-date *Archaeopteryx* by 70 million years, it's also not a dinosaur, let alone a theropod.

Most palaeontologists are not convinced. Interestingly though, Jones *et al.* came up with their idea *prior* to the discovery of scale-like tail feathers in two early birds, *Protopteryx* and *Confuciusornis*. So maybe their interpretation isn't so far off, and the origin of feathers, or feather-like integumentary appendages at least, is more complicated than at first thought.

As most proponents of the dinosaurian origin of birds (and thus feathers) are quick to point out, all the fuzzy dinosaurs discovered so far are fleet-

The first indication that fuzzy dinosaurs once flourished in the foothills of north-eastern China came in the form of the exquisite fossils of *Sinosauropteryx* (far right). The dark structures running down the back and the upper surface of the tail of this 1.4-metre-long adult specimen are thought to be hollow, filamentous integuments, not dissimilar to the hair of mammals, only much thicker. In life (right) these 'proto-feathers' would have covered most of the body, tail and upper parts of the arms and legs of this lightly built predator.



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footed theropods. It is therefore from the theropods that birds are thought to have evolved. However, a newly described psittacosaurid dinosaur from Liaoning may soon change all that. Psittacosaurids are up-to-Sheep-sized ceratopsians, the group of four-legged, plant-eating, horned ornithiscian dinosaurs that include *Triceratops*. The new psittacosaurid—a species of *Psittacosaurus*—is represented by an almost complete skeleton and, like many other Liaoning fossils, impressions of the skin and other soft tissues are visible. Most of its body is covered in pebbly, tuberculate scales, similar to those seen on the underside of birds' feet. But what's got everyone in a flutter is a series of long, spiny filaments or bristles along its tail, reminiscent of vaneless quills. These cylindrical, possibly tubular, structures were anchored deeply in the skin, and their occurrence on the tail suggests they may have been used in display behaviour.

The discovery of these 'tail bristles' in a dinosaur so far removed from the group that is thought to have given rise to birds, has caused a furore in the palaeontological community, and will undoubtedly radically change the way we think about dinosaur skin. Indeed, some of the world's foremost dinosaur palaeontologists, including Mark Norell from the American Museum of Natural History, now believe that *all* dinosaurs probably had feathers during some stage of their life cycle. Their reasoning goes something like this. If the two great branches of the dinosaur family tree, the saurischians and ornithiscians, each include members that were covered in feather-like integumentary structures (theropods and ceratopsians respectively), then it's likely their common ancestor, and thus all its descendants, also possessed them. Yet most of the fossil evidence to date doesn't appear to support this assumption. Natural moulds of skin belonging to several types of sauropods (including embryonic ones; see "Baby Behemoths", *Nature Aust.* Spring 2002), duck-billed dinosaurs and even a large theropod are now known. Just last year a spectacular, partially mummified duck-billed dinosaur was discovered in Montana. Typically, the skin of these animals is pebbly—similar to that seen on the limbs and body of the bristle-tailed *Psittacosaurus*. In no instances are there any traces of feathers.

On the face of known fossil evidence, it's now probably safe to assume that, despite their complexity, feathers or feather-like structures evolved more than once among dinosaurs. Linking feathers to the origin of birds, or even to theropods, could therefore be a bit presumptuous. It's possible that many dinosaurs, theropods among them, had a type of keratinous scaly covering that could easily transform into various types of feather-like structures. In some theropods these structures eventually transformed into the feathers we now associate with birds, and the arms on which these feathers sprouted into flapping wings. Other dinosaurs may have remained fuzzy. In the big evolutionary scheme of things, a feathery covering may not be as uniquely avian as we have come to believe. □

FURTHER READING

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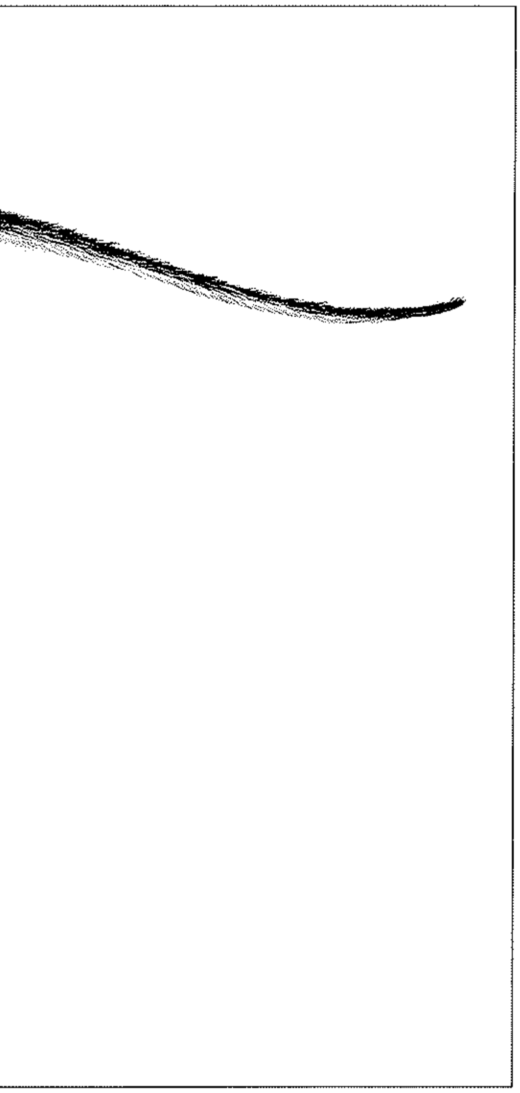

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