progressed in chronobiology from (presumed) status of metaphysics to molecular insights into mammalian clock genes.

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The riddle of the avian ancestry

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The hot topic today in palaeontology is the postulated dinosaur–bird link. The participants in the controversy have pointed out a variety of physiological and anatomical traits to swing the views for a pro- or anti-dinosaur ancestry for the modern birds. How the essentially ground-based animals adapted their skeletal framework and gradually developed feathers and took to air has been a fascinating question engaging avian palaeontologists since the discovery of *Archaeopteryx*, the first bird-like fossil with a few reptilian features in Germany in 1861 (Figure 1). In the process of launching them into air, nature had apparently experimented and evolved many intermediate species with characters that can be interpreted in favour of one or the other theories going around then. For a long time, palaeontologists viewed the Jurassic period *Archaeopteryx* as unquestionably the first bird to flap its wings in the skies, but discoveries of bird fossils in still earlier geological times, hinted evolution of flight, perhaps even in the Triassic, and *Archaeopteryx*, the bird pioneer was dethroned. Several new finds of avian fossils have inundated literature during the past few years from diverse countries[1–4] and they have not only added a fund of data about evolutionary trends, but in their wake, fueled the ongoing controversy about the reptile–dinosaur–bird evolution. Today, what portends to be last straw for the anti-dinosaurian paternity camp has now surfaced in the reported find of a feathered dinosaur fossil in China[5] and this has further exacerbated their already ruffled feathers.

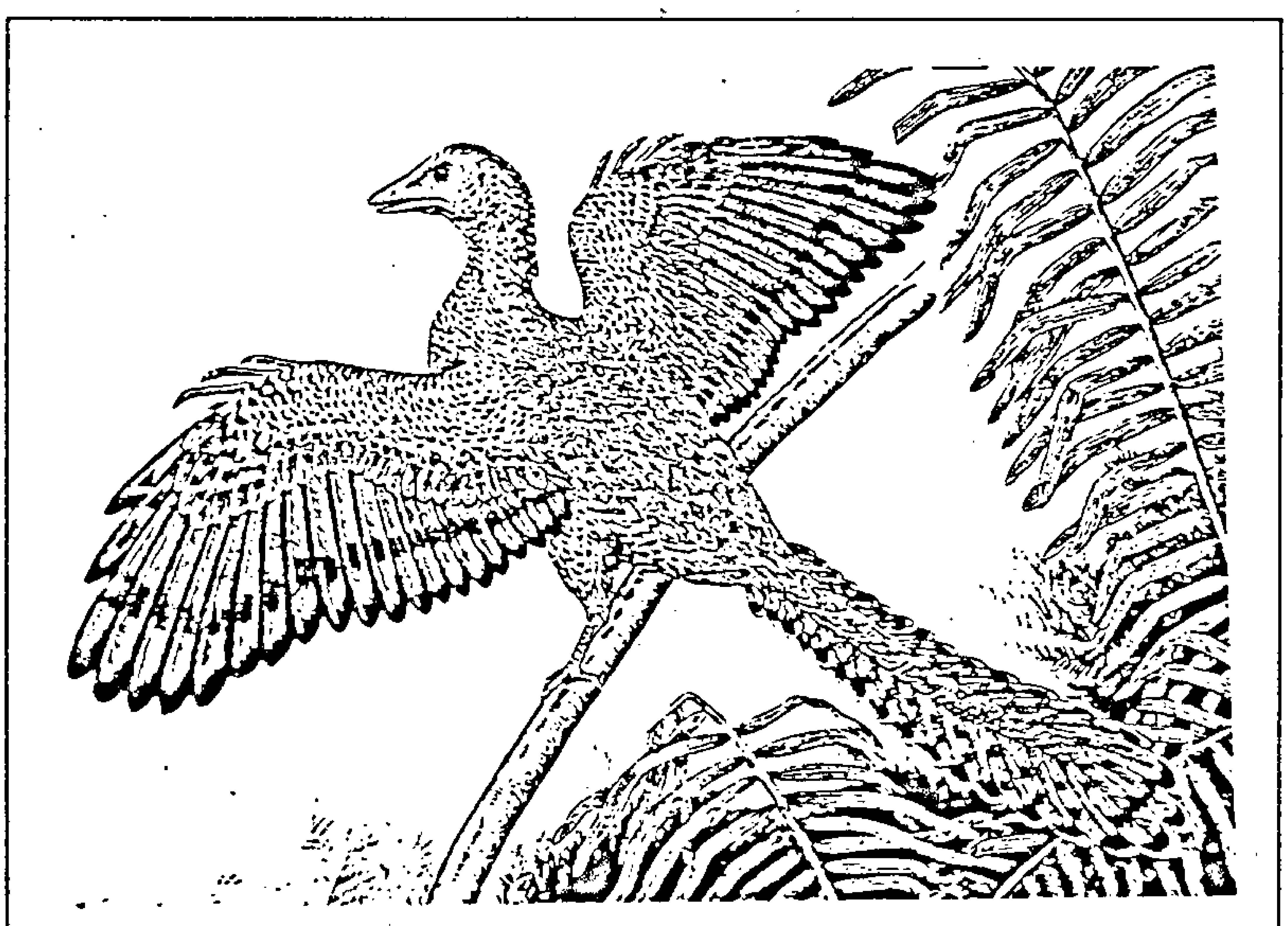

Figure 1. *Archaeopteryx*, the first bird fossil showing clawed wings, toothed beak and reptilian tail with feathers.

Compatible physiology and skeletal anatomy were two dominant aspects most palaeontologists were highlighting in their arguments for or against dinosaur pedigree for birds. Modern birds have skeletal framework specially suited for flight, like air-filled bones for buoyancy, a fused collar bone, breast bone with a deep keel for anchoring the flight muscles, lengthened forelimb (wing) with wrist and fused fingers and a composite pelvis and backbone with a remnant of a tail or pygostyle (Figure 2). Earlier scientists were, therefore, searching for evolutionary trends towards these skeletal modifications among some of the reptiles or dinosaurs they were suspecting as the ancestors. However, for

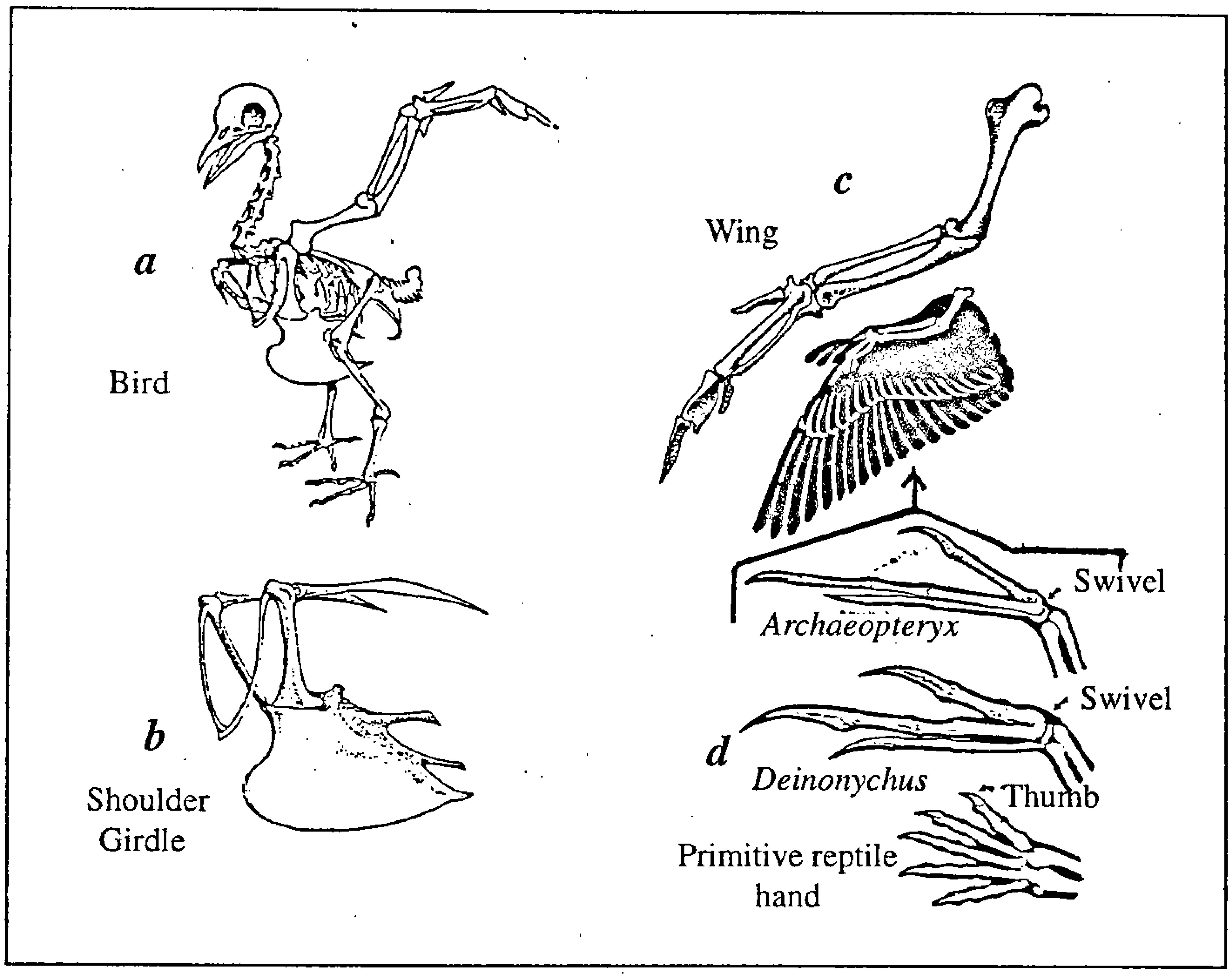

Figure 2. Bone characteristics of modern birds: ***a***, bird skeleton; ***b***, Shoulder girdle, breastbone with keel; ***c***, forelimb (wing) with wrist and fused fingers; ***d***, evolution of primitive reptile finger to fused wing bone.

every argument advanced in favour of one view, there were counter arguments from the opposite group also and tracing the ancestor of birds has remained inconclusive to this date.

In the nineteenth century, one of the broad divisions of the vertebrates centered around the animal's capacity for body heat production and its ability to maintain constant temperature over long periods, i.e. whether an animal is endothermic (warm blooded) or ectothermic (cold blooded). Birds and mammals are endothermic and their metabolism enables them to maintain a constant body temperature and be active always. In contrast, the metabolism in reptiles and amphibians is ectothermic and much influenced by the ambient weather – sluggish, when it is cold and, active, when hot. For a long time, the dinosaurs were classified as cold blooded or ectothermic reptiles. But based on certain characteristically endothermic micro structures called haversian canals, their bones display (tiny channels for blood vessels), and absence of growth rings as well as ambient or body temperature influenced ^{18}O – ^{16}O ratios in them (bones of endotherms show enrichment of the lighter ^{16}O isotope while the ectothermic ones are enriched in the heavier ^{18}O) the dinosaurs were considered as endotherms. Such a label also appeared quite logical as these animals had reigned the Earth for 140 million years competing and outclassing even the mammals of the period, a feat unlikely if they were sluggish ectotherms[6].

The view about the warm-bloodedness of dinosaurs prevailed for quite some time, but in recent years a few have started questioning it. Experiments conducted with live animals at Harvard University by Tomasz Owerkowicz have indicated that the development of the haversian canals is not so typical of endotherms as claimed; also, John Ruben at Oregon State University found that endothermic animals had wider nostrils and more typically, special sets of nasal bones called maxilloturbinals. These are thin bony or cartilaginous layers in their nasal passage which enable the animal to conserve water loss during exhalation by effectively condensing moisture in the air breathed out and recycling it back into the respiratory tract (a great necessity for the endotherms with their high metabolic rate). These dehumidifiers are absent in the cold-blooded reptiles and surprisingly not seen in the skulls of dinosaurs, even under computerized tomographic scanning (CT-scan). Ruben's calculations proved that the high activity of endotherms can be achieved by the ectotherms also, though in short bursts, and a few had even the capacity to retain heat for a considerable period. Accordingly, the dinosaurs were considered as ectotherms.

The type of dinosaur's metabolism thus appeared to be inapplicable in fixing the ancestry of birds and inferences in this regard from skeletal similarities, therefore, appealed to the scientists. In the later half of the nineteenth century, O. C. Marsh, of Yale University, found in a Cretaceous chalk formation in Kansas, fossil birds with teeth (*Hesperornis* and *Ichthyornis*) resembling those of a crocodile – sharp, curved with deep roots and also having skeletal aspects such as powerful wing-bones and bird-like vertebral column, all of which led him to attribute reptilian ancestry for birds[7]. This was also the time when the first bird fossil *Archaeopterix* was being much discussed. This fossil of the latter Jurassic bird showed well-preserved impressions of tail feathers and complete skeleton resembling very closely the medium-sized dinosaur *Ornitholestes* with long hind legs, typical reptilian tail, and a skeletal framework more primitive than the Cretaceous toothed birds of Marsh. To scientists of the period, in particular to Charles Darwin, these finds of semi-reptilian birds represented the evolutionary links in the march of the primitive reptiles to the Class Aves.

The famous zoologist, and a contemporary of Charles Darwin, Thomas Huxley documented various incontrovertible anatomical traits found in several fossil finds linking birds to certain meat-eating dinosaurs, such as the bird-like bipedal locomotion, typical ankle joints, toe pattern, ilium (upper hip bone), air cavities in the vertebral bones, highly mobile neck, long hind legs and reversed pubic bone[7]. The nearest ancestor was thought to be the small chicken-sized *Compsognathus* or the beaked dinosaur. With such strong indicators, the dinosaur connection for birds was generally accepted. However, to some palaeontologists who believed dinosaurs to be cold-blooded and hence incapable of supporting the energetic activities required for flight, such a link appeared incompatible with their physiology. The latter group of disbelievers derived support also from the just published book *The Origin of Birds*, by Gerhard Heilmann in 1925, in which the dinosaur–bird link was rejected on the ground that the functionally very important collar bone along with the modified shoulder pattern was totally absent in them or at best reduced and this was considered to go against such an evolution. On the other hand, the author felt that both birds and dinosaurs must have evolved as separate branches from a common ancestor having advanced characteristics of both dinosaurs and birds, like the predatory Triassic reptile called *Pseudosuchians* (false-crocodiles, e.g. *Ornithosuchus*). According to him, dinosaurs were mere cousins of birds and not their ancestors.

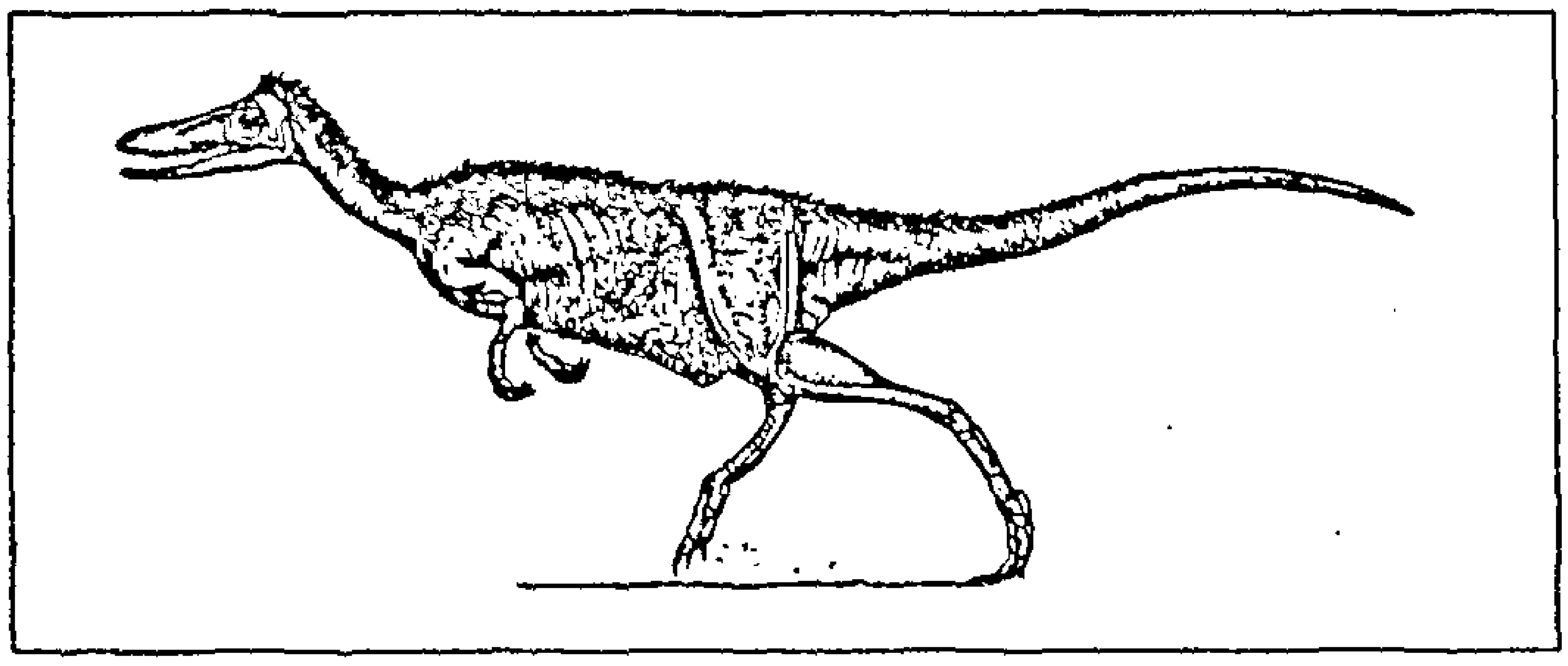

Figure 3. Dinosaur, discovered in Liaoning Province, China, showing a mane of downy feathers along neck, back and tail.

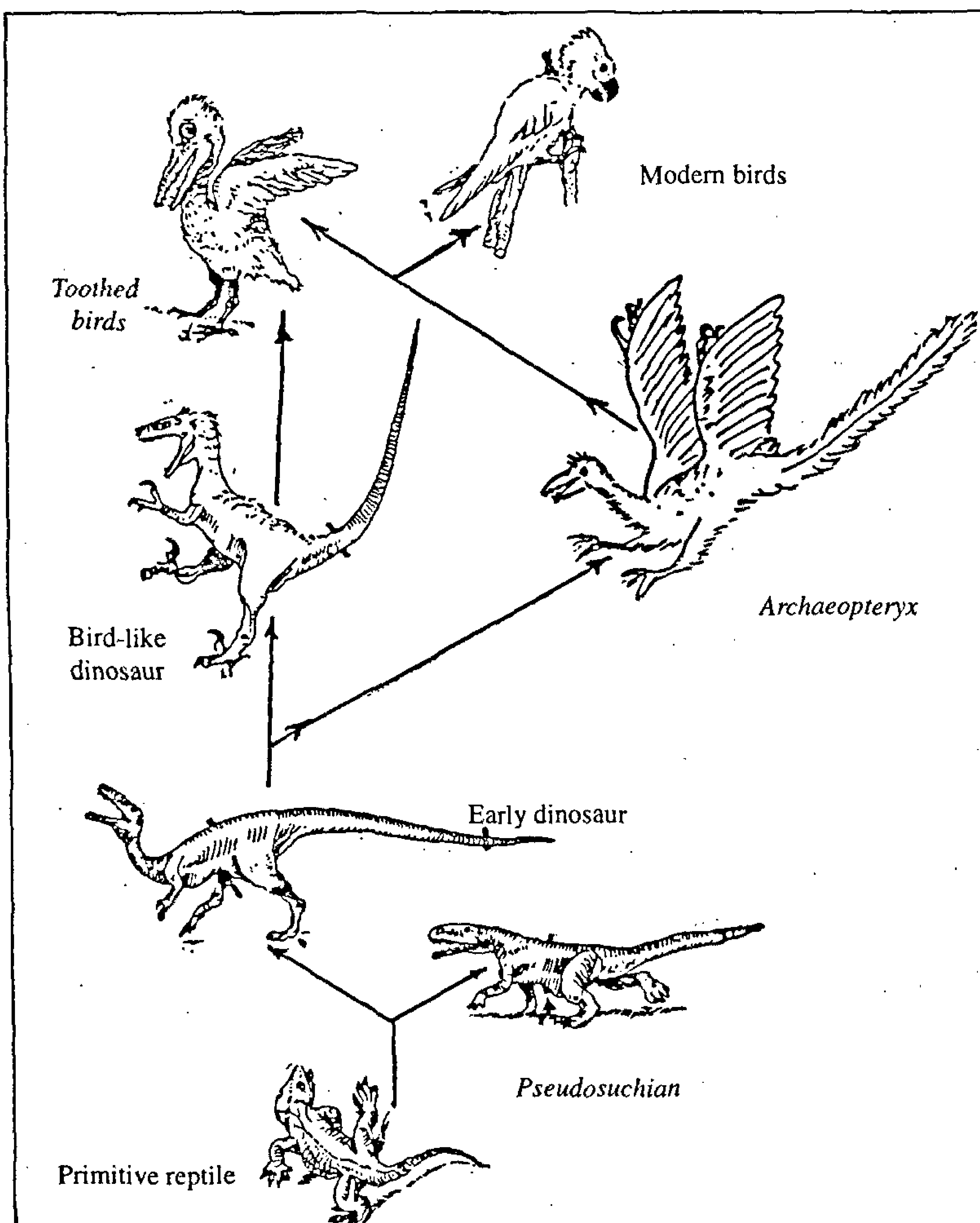

Figure 4. Evolutionary routes advanced for birds (adapted from Bakker[7]).

Four decades later, it was time for the pendulum to swing back, to the pro-dinosaur camp. In 1964, John Ostrom of Yale, came across a few *Archaeopteryx* fossils in a Dutch museum, showing long bony fingers with sharp claws complete in all biomechanical aspects with those of a warm-blooded carnivorous dinosaur *Deinonychus* (grouped under Theropods dromaesaurid and coelurosaurs). The match was perfect even in details about shoulder, hip, thigh, wrist bone assembly and ankle all of which were modifications specially adapted for birds, notably the ground based ones. The three separate fingers (a short thumb and two longer fingers) of *Deinonychus* and *Archaeopteryx*, according to him, became a single fused bone in modern birds (Figure 2 *d*). This evolutionary modification is clearly reflected even today in unhatched chicks in which these fingers remain separate, an undoubted hangover or vestige pointing to their dinosaur ancestry. He felt that the wings were developed initially for gliding or sweeping prey into the mouth, and gradually got modified to power flight[7]. In a recent discovery[11] in Patagonia (Argentina) an intermediate form filling the gap between *Archaeopteryx* and the Theropod *Deinonychus* has come up reinforcing once again the dinosaur–bird link, though a few skeptics continue to dispute several of these pro-dinosaurian views.

In August 1996, Chinese palaeontologists unearthed from Liaoning province in northeastern China a meter-long fossilized skeleton of a small dinosaur covered with what distinctly appeared to be feathers, preserved in a volcanic formation (Yixian formations) dated around 140 to 120 million years[5]. This fossil, presently in China, was examined by leading Chinese and Western experts and photographs were presented at the 56th Annual Meeting of the Society of Vertebrate Palaeontology, held in New York in October 1996. The fossil named *Sinosauropteryx prima* showed a mane of downy feathers along the neck, back and tail, a feature hitherto seen only in bird fossils. It appeared to be a close relative of *Compsognathus*, a dinosaur which Ostrom had earlier strongly favoured as the probable ancestor. Soon two more such feathered fossils were discovered from the same site, thus making available three specimens for evaluation. This fossil exhibiting feathers was the link the pro-dinosaurians were looking for and the find has, no doubt, galvanized them. However their euphoria may turn out to be short lived if one goes by the findings of Ostrom and colleagues whose re-examination of this Chinese fossil, a few months back, has cast doubts on the identity of feathers; they feel that these are actually 'long parallel arrays of fibres that lack branching patterns of modern feathers'[8].

Today, the staunch critics of dinosaur–bird descent are Alan Feduccia of the University of North Carolina and Larry Martin of University of Kansas along with colleagues Zhonghe Zhou and Linhai Hou of the Chinese Academy of Sciences who had all doubted the identification of feathers; besides, they had felt that it is 'biophysically impossible to evolve flight from such large bipeds with foreshortened limbs and heavy balancing tails', all wrong anatomies for flight[9,10]. Instead they probably could have descended from a common ancient reptile that gave rise to both birds and dinosaurs, a view similar to Gerhard Heilmann's in the 1920s. According to Feduccia and Martin, the recent fossil bird finds from China[1] – *Liaoningornis* and *Confuciusornis* which predate *Archaeopteryx* – show features distinctive of endothermic physiology and a different bone formation on their feet, rib cage, sternum and shoulder. These, they say, clearly indicate that the tree of avian evolution had side branches – one led to the modern birds while another to *Archaeopteryx* type of birds, both of distinctly different taxa. This group feels that the first bird must have flown some 76 million years before the arrival of bird-like dinosaurs during late Cretaceous, thus questioning dinosaurian origin for modern birds[10].

There is, however, one issue vital to the view of Feduccia and others and this pertains to the validity of age of the fossil which, of course, is the age of the Yixian formations from where they were collected. Recent argon-argon dates indicate an age of 121 m.y. only and not 137–142 m.y as earlier thought, which will, therefore, put these Chinese bird fossils younger to Jurassic as well as to *Archaeopteryx* and the dinosaurs. Feduccia remains unperturbed by this dating controversy, relying more on the fact that both types of birds with distinct skeletal anatomies are met with in post-*Archaeopteryx* period which is strongly supportive of the dichotomy, he has envisaged, in avian evolution[9].

In spite of the finds already of dinosaur fossils from diverse countries – Madagascar, Patagonia, Spain besides China with many bird-like features such as wrist bones, claws, fused fingers, breast bones, clavicles, shoulder, folding arms and other skeletal similarities, apart from the recent, feathered dinosaur from Yixian Formation (notwithstanding the latest findings to the contrary), now more reliably dated, the enigma about bird ancestry and the evolutionary route they have taken (Figure 4) does not appear to diminish. Though their dinosaur link seems to be gathering strength, if not established beyond doubt, what appears to be misunderstood by many is that such a paternity is current only to a few of the dinosaur species which have undoubted primitive avian anatomy. There remain still a few loose ends in the evolutionary ascent of birds, defying a consensus among the palaeontologists such as the question of endothermy or ectothermy of the avian ancestors, functional modifications in the anatomy transition to flight, and about the development of flight itself, whether the parachuting or gliding reptiles adapted themselves for this or whether the modern birds descended from a side branch to the main avian tree that sprouted from a Triassic animal. Currently the view that has wide acceptance is the dinosaur ancestry for birds, and as Robert Bakker had observed, somewhat paradoxically, 'dinosaurs are not extinct; one species has survivors – they are the birds[6]'.

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