the sub-microsecond timescale, even given the considerable distance between the ruthenium complex and the stations (which also slows down the rate of the forward electron-transfer reaction). In fact, the charge-separated state has an average lifetime of around 10 microseconds.

Reduced bipyridinium is a very much poorer binding site for the ring, and the charge-separated state survives long enough for about 10% of the rings to undergo significant brownian motion. Detailed balance is broken and a net flux of rings occurs as they shift their allegiance to the unreduced station 2. After 10 microseconds, however, as back electron transfer finally takes place, station 1 regains its stickiness. A net flux of rings occurs back from station 2, the system returns to its original equilibrium, and a machine cycle has taken place. The process can be repeated for at least a thousand cycles.

This is a fascinating system, working (as do most other light-driven shuttles[2,5–8]) without the consumption of chemical fuels or the formation of waste products. It can be properly called a machine because component displacements occur in response to an external stimulus. But is it really best described as a 'nanomotor'? Chemists are still pondering the most useful way to understand the behaviour of the contemporary, early generations of synthetic molecular machines, but physics and biology offer many useful phenomenon-based ideas in this regard. Brownian motors, for example, use mechanisms[9] that harness random molecular-level motion like that of the ring motion in rotaxanes.

Such brownian ratchet mechanisms, which are believed to account for the behaviour of some motor proteins[10], all require detailed balance to be broken to allow a net, directed flux of particles. Crucially, however, the 'ratchet' part of the mechanism ensures that the resulting change in particle distribution is not undone when the motor is reset. This allows the machine to be able to pump the particle distribution further and further away from equilibrium (as with the enzymes that synthesize the currency of intracellular energy transfer, ATP) or move itself progressively down a track (as with the cell's internal packhorse, kinesin).

This feature is missing from Balzani and colleagues' rotaxane[1], and other simple molecular shuttles[2,5–8]: the work done in breaking detailed balance is undone by the reset step. For such a system to be understood to be a motor by a statistical physicist or biologist, therefore, the rings would have to be diverted along a different track during the reset phase (making a rotary motor), or remain where they are while the machine is reset (making a linear motor or pump). The former is the basis of several wholly synthetic molecular motors[11–15]; the latter has thus far been achieved only with artificial structures made from DNA[16].

Balzani and colleagues' shuttle operates through a fully autonomous photochemical cycle; but can these molecules repetitively do work as long as sunlight is available? The authors did not use sunlight in the experiments they report, but instead treated the rotaxanes with a single 10-nanosecond laser pulse at a visible-light wavelength. If continuously irradiated with sunlight, the distribution of the rings between the two stations would reach a steady state (the exact distribution depending on the intensity of the light) within a few milliseconds. To generate net flows of rings between the stations after that, it appears one would have to switch the light source rapidly on and off.

This is in contrast to the performance of another family of machine molecules that have components that rotate directionally, rather than shuttle linearly[12,17]. When these rotary molecules reach a steady state under continuous irradiation, as with the rotaxanes the bulk distribution of the machine components no longer changes. But even at the steady state, at a sufficiently high temperature, net fluxes of the rotor components still occur through different pathways between four different rotary isomers that are present. Under constant irradiation, the molecules thus operate continuously as directionally rotating motors[17].

Synthetic molecular motors and machines are very much in their infancy, and chemists are still learning the most basic rules for their design and operation. It is a field that can usefully draw on input from physicists, biologists, engineers and materials scientists. For a deeper understanding of molecular machine systems to evolve, therefore, it would be highly beneficial if the terminology used to describe them were to become consistent across all the contributing disciplines. Balzani and colleagues' latest photochemical experiments[1] represent a fascinating advance in our understanding of how a charge-separated state can be used to bring about a nuclear displacement in a unimolecular machine. It will doubtless prove an important stage on the route towards autonomous artificial nanomotors powered by sunlight. ■

Euan R. Kay and David A. Leigh are in the
School of Chemistry, University of Edinburgh,
King's Buildings, West Mains Road,
Edinburgh EH9 3JJ, UK.
e-mail: david.leigh@ed.ac.uk

1. Balzani, V. *et al. Proc. Natl Acad. Sci. USA* **103,** 1178–1183 (2006).
2. Brouwer, A. M. *et al. Science* **291,** 2124–2128 (2001).
3. Ashton, P. R. *et al. Chem. Eur. J.* **6,** 3558–3574 (2000).
4. Onsager, L. *Phys. Rev.* **37,** 405–426 (1931).
5. Murakami, H., Kawabuchi, A., Kotoo, K., Kunitake, M. & Nakashima, N. *J. Am. Chem. Soc.* **119,** 7605–7606 (1997).
6. Wurpel, G. W. H., Brouwer, A. M., van Stokkum, I. H. M., Farran, A. & Leigh, D. A. *J. Am. Chem. Soc.* **123,** 11327–11328 (2001).
7. Altieri, A. *et al. Angew. Chem. Int. Edn* **42,** 2296–2300 (2003).
8. Wang, Q.-C., Qu, D.-H., Ren, J., Chen, K. & Tian, H. *Angew. Chem. Int. Edn* **43,** 2661–2665 (2004).
9. Reimann, P. *Phys. Rep.* **361,** 57–265 (2002).
10. Astumian, R. D. *Science* **276,** 917–922 (1997).
11. Kelly, T. R., De Silva, H. & Silva, R. A. *Nature* **401,** 150–152 (1999).
12. Koumura, N., Zijlstra, R. W. J., van Delden, R. A., Harada, N. & Feringa, B. L. *Nature* **401,** 152–155 (1999).
13. Leigh, D. A., Wong, J. K. Y., Dehez, F. & Zerbetto, F. *Nature* **424,** 174–179 (2003).
14. Hernández, J. V., Kay, E. R. & Leigh, D. A. *Science* **306,** 1532–1537 (2004).
15. Fletcher, S. P., Dumur, F., Pollard, M. M. & Feringa, B. L. *Science* **310,** 80–82 (2005).
16. Kelly, T. R. *Angew. Chem. Int. Edn* **44,** 4124–4127 (2005).
17. Feringa, B. L., Koumura, N., van Delden, R. A. & ter Wiel, M. K. J. *Appl. Phys. A* **75,** 301–308 (2002).

PALAEONTOLOGY

Scales, feathers and dinosaurs

Xing Xu

A fossil dinosaur that 'nests' with feathered relations in the dinosaur phylogenetic tree did not, it seems, have feathers. The discovery will encourage a re-evaluation of feather evolution.

Only birds have feathers — or so we thought until the discovery of fossils of feathered dinosaurs in China and elsewhere[1]. Since then, palaeontologists and biologists have together been painting a simple picture of feather evolution based on evidence from fossils and from developmental biology. A new example of a predatory dinosaur, described by Göhlich and Chiappe on page 329 of this issue[2], makes that picture a little bit more complicated.

The context is provided by Figure 1 (overleaf), which shows the generally understood relationships among the main groups of dinosaur (Aves — the birds — is the only one of these groups to have extant members). Feathers are thought to be characteristic of the Coelurosauria, a group of theropod dinosaurs that includes Aves and several other groups. Because feathers are unique and therefore innovative in developmental and evolutionary terms[3], we can infer their presence in extinct forms using a method called phylogenetic bracketing. Based on the presence of feathers in some extinct coelurosaurs and all living birds, this approach suggests that all coelurosaurs, with the possible exception of gigantic species such as *Tyrannosaurus rex*, are feathered[4].

The small coelurosaur described by Göhlich and Chiappe now enters the picture. This new dinosaur, a carnivore named *Juravenator*, is represented by a beautifully preserved skeleton collected from Late Jurassic deposits from Solnhofen, Germany — the source of all specimens of the earliest-known bird *Archaeopteryx*. At 151 million to 152 million years old, the deposits in which *Juravenator* was found are only 2 million to 3 million years older than those containing *Archaeopteryx*.

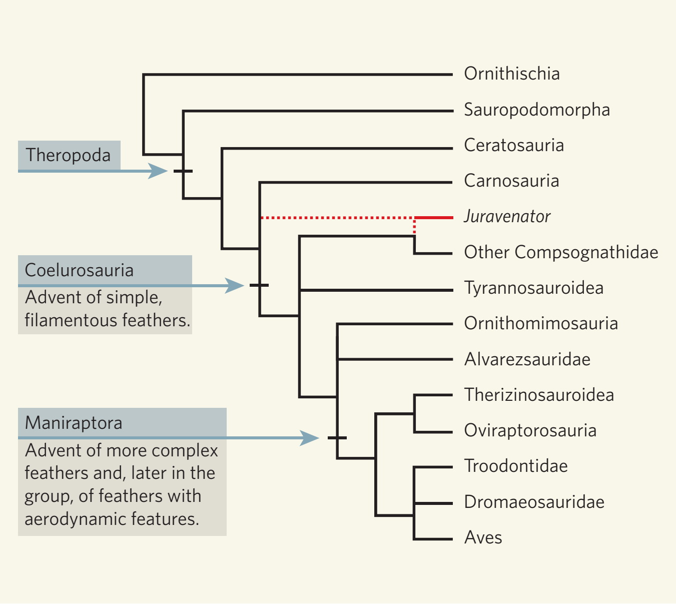

Figure 1 | Dinosaurs and feather evolution. This evolutionary tree of dinosaur groups is compiled from several phylogenetic analyses[6–9], and shows the possible occurrence of the main events in feather evolution. The tree shows alternative positions for *Juravenator*, the new species described by Göhlich and Chiappe[2], among the theropods. A compsognathid affinity for *Juravenator* suggests that feathers evolved independently or were lost in some species early in coelurosaurian evolution, or that some coelurosaurs had limited feathery covering. If *Juravenator* turns out to be more 'basal' in the tree than the known feathered dinosaurs, it would suggest that feather evolution started during the early history of the Coelurosauria.

Given the worldwide rarity of complete specimens of small theropods from the Jurassic, the exceptionally well-preserved skeleton of *Juravenator* is in itself a notable find. Most significantly, however, the specimen preserves scaled skin around the tail and hindlimbs. This is a big surprise considering that *Juravenator* is a small coelurosaur and a member of a small group called the Compsognathidae — which includes the first known feathered dinosaur, *Sinosauropteryx*, the tail and hindlimbs of which were feathered[5].

The evolution of biological structures must be studied within an evolutionary framework. In the case of feathers, a robust theropod phylogeny is the basis for reconstructing the sequence in which feathers evolved. The distribution of various feather morphologies on the currently accepted phylogeny[6–9] suggests that simple, filamentous feathers first evolved no later than the earliest stage of coelurosaurian evolution. More complex feathers with a thick central shaft and rigid symmetrical vanes on either side appeared early in the evolution of the coelurosaurian group Maniraptora; and feathers with aerodynamic features, such as a curved shaft and asymmetrical vanes, appeared within the maniraptors but before the origin of birds[4]. This inferred sequence of events is supported independently by developmental data[3,10]. Göhlich and Chiappe[2] place *Juravenator* within the Compsognathidae, a group that is 'basal' in the coelurosaurian tree (Fig. 1). So *Juravenator* should bear filamentous feathers. But it seems to be a scaled animal, at least on the tail and hind legs.

Why, then, does a member of a feathered dinosaur family bear scales? The authors' answer[2] is straightforward: feather evolution, they say, is more complex than we thought. This could well be so. The early evolution of some major structures — such as the incorporation of jaw suspensory bones into the middle ear of mammals — is often flexible and experimental. It would not be surprising if feathers were lost and scaly skin re-evolved in some basal coelurosaurian species, or if feathers evolved several times independently early in coelurosaurian evolution. Or perhaps, suggest Göhlich and Chiappe, the absence of feathers on body parts that are feathered in other coelurosaurs is due to variability in the extent of a feathery covering among coelurosaurs. Although modern birds are extensively feathered, this may not have been true of their remote extinct relatives.

Feather preservation is extremely rare and biased. For example, contour feathers — those feathers forming the general covering of a bird — are not seen in some otherwise beautifully preserved specimens of *Archaeopteryx*, but are evident in other examples[11]. Even after the discoveries of so many fossils of feathered dinosaurs, we still have only a patchy picture of feather distribution in basal coelurosaurs. And many details are missing — for example, we don't know whether the hooked structures known as barbules are present in some types of feathers, and how exactly feathers covered dinosaurian bodies. Göhlich and Chiappe propose that *Juravenator* could be evidence that the bodies of some basal coelurosaurs were more scaly than those of living birds, which have scales only on their lower legs. This explanation is the most likely, given that the authors have carefully examined and analysed the specimen. Yet other possibilities exist.

For example, if *Juravenator* in fact lies more basally than the Compsognathidae in the theropod tree (Fig. 1), we would have a clearer picture of feather evolution instead of this complicated story. We know that feathers appeared at least as early as the divergence of the Compsognathidae from the main trunk of the theropod tree, but we don't know yet when they first evolved, owing to the poor fossil record. The scaled *Juravenator* would then be a starting point for feather evolution.

In my opinion, this possibility cannot yet be ruled out. First, the evidence[2] supporting a compsognathid affinity for *Juravenator* is not very strong. Second, the description of *Juravenator* is based on a juvenile specimen, some features of which are likely to have pulled the species up the tree if *Juravenator* followed the developmental patterns revealed by certain other theropod specimens[12]. Finally, although they agree in most respects, the proposed relationships[6–9] between the theropods themselves are not entirely stable.

Whatever the explanation, our knowledge of early feather evolution has been enriched by the discovery of *Juravenator*. Moreover, the discovery emphasizes where future research might fruitfully be concentrated. The Middle-to-Late Jurassic, between about 176 million and 146 million years ago, was a critical time for the origins and early evolution of the coelurosaurian lineages, including birds. But the fossil record is poor, and any new coelurosaur from this period adds considerably to our understanding of the group. *Juravenator* may complicate the picture, but it makes it more complete and realistic. ■

Xing Xu is at the Institute of Vertebrate
Paleontology and Paleoanthropology,
Chinese Academy of Sciences,
142 Xiwai Street, Beijing 100044, China.
e-mail: xu.xing@ivpp.ac.cn

1. Norell, M. & Xu, X. *Annu. Rev. Earth Planet. Sci.* **33,** 277–299 (2005).
2. Göhlich, U. B. & Chiappe, L. M. *Nature* **440,** 329–332 (2006).
3. Prum, R. O. & Brush, A. H. *Q. Rev. Biol.* **77,** 261–295 (2002).
4. Xu, X. *Integrative Zool.* (in the press).
5. Chen, P. J., Dong, Z. M. & Zhen, S. N. *Nature* **391,** 147–152 (1998).
6. Sereno, P. C. *Science* **284,** 2137–2147 (1999).
7. Norell, M. A., Clark, J. M. & Makovicky, P. J. in *New Perspectives on the Origin and Evolution of Birds* (eds Gauthier, J. & Gall, L. F.) 49–67 (Yale Univ. Press, 2001).
8. Holtz, T. R. Jr *Gaia* **15,** 5–61 (2000).
9. Rauhut, O. W. M. *The Interrelationships and Evolution of Basal Theropod Dinosaurs* Spec. Pap. Palaeontol. **69** (Palaeont. Ass., London, 2003).
10. Yu, M.-K., Wu, P., Widelitz, R. B. & Chuong, C.-M. *Nature* **420,** 308–312 (2002).
11. Wellnhofer, P. in *Feathered Dragons — Studies on the Transition from Dinosaurs to Birds* (eds Currie, P. J., Koppelhus, E. B., Shugar, M. A. & Wright, J. L.) 282–300 (Indiana Univ. Press, 2004).
12. Xu, X. *et al. Nature* **439,** 715–718 (2006).