brackish facies. In a falling sea-level sequence the following biosedimentological facies sequence can be expected within the core: 1, open marine; 2, shallow marine; 3, marginal marine; and 4, brackish conditions. The last three facies are seen, for example, in the lower part of core 5 (Fig. 1b). When sea level rises the sequence reverts to marginal marine and then to shallow marine. It is this sequence of facies changes before and after the deposition of the brackish-water sediments that determine the position and duration of shallow-water conditions. The four depositional sequences are as follows.

"Open marine" was identified by the presence of fragile pteropod remains, numerous and diversified benthic foraminifer and ostracod taxa, that are indicative of normal marine salinity. In analogy with modern conditions, water depths are around 20 m because planktonic foraminifers are either absent or rare.

"Shallow marine" was characterized by the absence of pteropods and the presence of numerous and well-preserved foraminifer and ostracod taxa (which include species of *Aglaiella*, *Argilloecia*, *Callistocythere*, *Loxoconcha*, *Pterygocythereis*, *Uloleberis*, in addition to common bairdiid taxa); there are no planktonic foraminifers. Biodiversity of the microbiota is substantially lower than in the open marine facies. Water depths are around 10 m.

"Marginal marine" was defined by a change to a lower diversity of benthic marine ostracods (commonly encountered species: *Neocytheretta* ssp., *Xestoleberis* sp.) and benthic foraminifers, accompanied by the robust endobenthic scaphopods. Most specimens show signs of abrasion. Bivalve molluscs are common and frequently damaged. Broken echinoid spines and bryozoan remains are ubiquitous. Terrigenous material, mostly quartz, is common. Water depths are less than 5 m, being within the zone of tidal influence.

"Brackish water" was identified by a paucity of typically marine organisms and the presence of the foraminifer *Ammonia beccarii*, often in large numbers—and as dwarf morphs due to environmental stresses such as fluctuating salinities and temperatures—accompanied by the euryhaline ostracods *Cyprideis australiensis*, *Leptocythere* spp. and *Neocytheretta* spp. Signs of bleaching of the calcareous shells, indicating exposure to corrosive waters, are common. Terrigenous material is common. Salinities are well below sea-water salinity due to a strong influence of continental waters, such as found in estuaries and tidal flats. Water depths correspond to near mean sea level and up to the high-tide level. Present tidal range is ±3 m and this represents the upper limit of the accuracy of these sea-level indicators.

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Cursoriality in bipedal archosaurs

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Modern birds have markedly foreshortened tails and their body mass is centred anteriorly, near the wings[1–5]. To provide stability during powered flight, the avian centre of mass is far from the pelvis, which poses potential balance problems for cursorial birds. To compensate, avians adapted to running maintain the femur subhorizontally, with its distal end situated anteriorly, close to the animal's centre of mass; stride generation stems largely from parasagittal rotation of the lower leg about the knee joint[6–12]. In contrast, bipedal dinosaurs had a centre of mass near the hip joint and rotated the entire hindlimb during stride generation[4–8,11–13]. Here we show that these contrasting styles of cursoriality are tightly linked to longer relative total hindlimb length in cursorial birds than in bipedal dinosaurs. Surprisingly, *Caudipteryx*, described as a theropod dinosaur[14,15], possessed an anterior centre of mass and hindlimb proportions resembling those of cursorial birds. Accordingly, *Caudipteryx* probably used a running mechanism more similar to that of modern cursorial birds than to that of all other bipedal dinosaurs. These observations provide valuable clues about cursoriality in *Caudipteryx*, but may also have implications for interpreting the locomotory status of its ancestors.

In contrast to bipedal dinosaurs, the femur in cursorial birds contributes little to generation of stride length, and avian hindlimb movement is largely the result of retraction of the lower leg[7–12]. Hence, it might be expected that relative stride length in cursorial birds would be lower than that in bipedal dinosaurs. However, this is probably not the case—lengths of 'effective hindlimb' segments in birds (tibiotarsus + tarsometatarsus) and dinosaurs (femur + tibia + metatarsal III) are equivalent[16] (Fig. 1a). Consequently, total hindlimb length in cursorial birds is invariably one-and-a-half times longer than in theropod and ornithopod dinosaurs (Fig. 1b). Additionally, as adept avian runners have evolved repeatedly from flighted ancestors[17], we conclude that these profound anatomical modifications that facilitate avian cursoriality are multiple convergent responses to secondary resumption of cursoriality in distantly related taxa independently derived from flighted ancestors.

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Caudipteryx has been described as a feathered dinosaur[14,15] and therefore would be expected to have had a dinosaurian mechanism of cursoriality. However, relative total hindlimb proportions in *Caudipteryx* contrast sharply with those in all other bipedal dinosaurs and are indistinguishable from those in cursorial birds (Fig. 1b). Accordingly, based on the tight linkage of hindlimb proportions to cursorial mechanisms in bipedal archosaurs, we suggest that *Caudipteryx* ran using a mechanism more similar to that of modern cursorial birds than to typical dinosaurs. Significantly, lower leg (tibia + metatarsal) length in *Caudipteryx* is also the same as the 'effective hindlimb' length of cursorial birds, which is equivalent to total hindlimb length in theropods (Fig. 1a).

Because the relative hindlimb proportions of *Caudipteryx* are indistinguishable from those of cursorial birds, it was also likely to have had its centre of mass situated anteriorly, rather than posteriorly as in other dinosaurs. Importantly, an anterior, cursorial birdlike centre of mass in *Caudipteryx* is demonstrated by application of Henderson's mathematical–computational model for centre of mass in tetrapods[18]. This analysis indicates that the centre of mass in *Caudipteryx* was around 2.3 times more anterior to the acetabulum than in the dromaeosaurid theropod *Deinonychus* (Fig. 2).

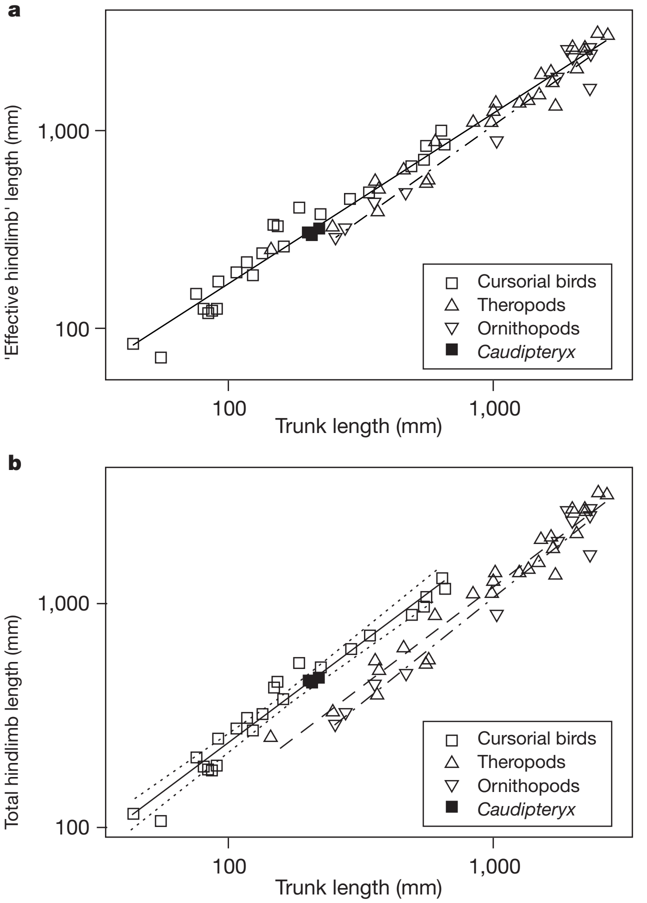

Figure 1 Hindlimb proportions in cursorial birds, theropod and ornithopod dinosaurs, and three specimens of *Caudipteryx*. **a**, The relation of trunk length (T) to 'effective hindlimb' length in bipedal dinosaurs (femur + tibia + metatarsal III), cursorial birds (tibiotarsus + tarsometatarsus) and *Caudipteryx* (tibia + metatarsal III). Cursorial avian and theropod 'effective hindlimb' length equals $0.50T^{0.87}$; for ornithopod dinosaurs it is $0.17T^{0.96}$ ($R^2 = 0.97$, $P < 0.0000$). Extra sum of squares F-test determined that regressions for cursorial bird effective hindlimb length and theropod dinosaur total hindlimb length are indistinguishable ($F_{(2,60)} = 3.654$; $P < 0.05$). Solid line, regression for cursorial birds and theropod dinosaurs; dashed-dotted line, regression for ornithopod dinosaurs. **b**, The relation of trunk length (T) to total hindlimb length in bipedal archosaurs (femur + tibia + metatarsal III in ornithopod and theropod dinosaurs; femur + tibiotarsus + tarsometatarsus in cursorial birds). Hindlimb length equals $0.38T^{0.90}$ for theropod dinosaurs, $0.17T^{0.96}$ for ornothopod dinosaurs, $0.58T^{0.90}$ for cursorial birds ($R^2 = 0.97$, $P < 0.0000$). Solid line, linear regression for cursorial birds. Dotted lines, 99% confidence intervals for cursorial birds. Dashed line, regression for theropod dinosaurs. Dashed-dotted line, regression for ornithopod dinosaurs. Values for *Caudipteryx* specimens were not included in regression calculations. See Methods for details.

An anterior centre of mass is consistent with the brevity of the tail of *Caudipteryx*, which is among the shortest, if not the shortest, of all bipedal dinosaurs. Additionally, as in cursorial birds but not dinosaurs, the dimunitive tail and the complete absence of a femoral fourth trochanter indicate that the caudofemoralis was not an important locomotory muscle. The likely absence of well developed caudofemoralis musculature indicates that the short tail may have been relatively narrow, with most of its musculature devoted to generating tail movement.

Of all the bipedal dinosaurs, only *Caudipteryx* possessed limb proportions and a centre of mass like those of cursorial birds and, by extension, a cursorial-bird-like running style. These observations might provide valuable clues about the lifestyle of *Caudipteryx* but they may also have implications for interpretation of its taxonomic affinities. We suggest that the anatomical uniqueness of *Caudipteryx* must be consistent with one of the following: (1) *Caudipteryx* was simply an unusual theropod dinosaur whose cursorial ancestors abandoned dinosaurian locomotion and assumed the unique morphology and running style of cursorial birds; (2) *Caudipteryx* was a theropod dinosaur derived from flighted ancestors; (3) *Caudipteryx* was a post-*Archaeopteryx*, secondarily flightless bird and not a 'feathered dinosaur'. The first alternative is supported by cladistic analyses that indicate that *Caudipteryx* was a coelurosauroid theropod[14,15]. However, none of these analyses has considered *Caudipteryx*'s extensive suite of cursorial-bird-like locomotory characters, and all other theropods were typically dinosaurian in this regard (Figs 1, 2). In this context, it is important to reiterate that the same locomotory specializations present in *Caudipteryx* and cursorial members of eight avian orders are tightly linked to the latter taxa having been derived from flighted ancestors. Accordingly, it is difficult to construct a hypothesis in which the terrestrial theropod ancestors of *Caudipteryx* might have switched to a specialized, running style with an anterior centre of mass, resembling that of

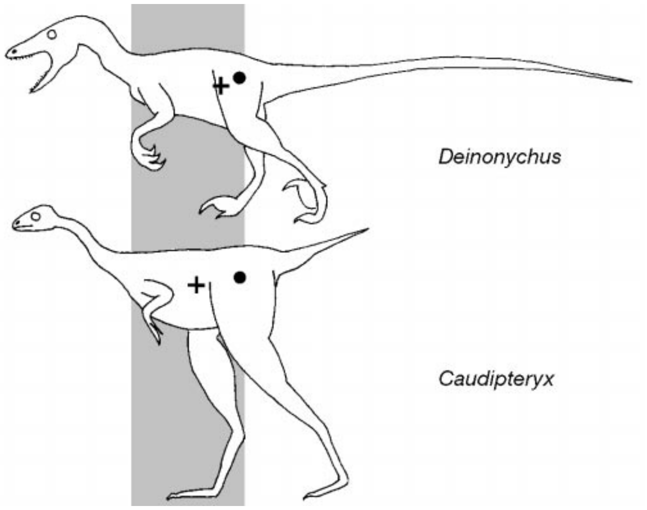

Figure 2 Estimated centre of mass for *Deinonychus* and *Caudipteryx*. Figures are scaled so that trunk lengths are equivalent. Relative to the acetabulum (dot), centre of mass (cross) in *Caudipteryx* approximates centre of mass in cursorial birds and is 2.3 times more anterior than in *Deinonychus*. *Deinonychus* modified from ref. 19. *Caudipteryx* was reconstructed from NGMC 97–4–A and NGMC 97–9–A. For illustrative purposes the femora of *Caudipteryx* have been drawn in a more dinosaurian position. The femora of *Caudipteryx*, as in cursorial birds, was probably more horizontal. See Methods and ref. 18 for details.

cursorial birds, when they were already adept cursors with a posterior centre of mass.

The second proposal, that some theropods were derived from currently unknown, flighted ancestors, has been suggested[19]. As noted above, *Caudipteryx*'s locomotory adaptations are consistent with it having been derived from flighted ancestors. However, there is no substantive evidence to support flighted ancestors for any other theropods. Nevertheless, this possibility cannot be dismissed. In the light of problems associated with theories (1) and (2), perhaps the third, that *Caudipteryx* was a secondarily flightless, post-*Archaeopteryx*, cursorial bird, deserves closer scrutiny than it has received so far. We find it a striking coincidence that the only unambiguously feathered theropod was also the only known theropod likely to have utilized locomotory mechanisms identical to those of cursorial birds. ☐

Methods

Hindlimb and trunk length data

We recorded data on hindlimb element (femur, tibia or tibiotarsus, metatarsal III or tarsometatarsus) and trunk lengths in mature, extant and extinct cursorial (or at least ground-living) birds (from eight orders and 24 genera, including tinamou, cassowary, ostrich, galliforms, roadrunners, bustards, moa and elephantbird) and 38 genera of theropod and ornithopod dinosaurs (see Supplementary Information). Data were collected from avian and dinosaur specimens in museum collections or obtained from published data and/or scale reconstructions. Individuals were included only if the hindlimb skeleton was adequately known and the trunk was sufficiently known that the describers were able confidently to reconstruct the specimen.

The morphometric data collected from each individual included maximum femoral length, maximum tibia (or tibiotarsus) length (excluding the cnemial crest) maximum metatarsus (or tarsometatarsus) length and trunk length. We defined trunk length as the distance from the first dorsal vertebrae and/or head of the first dorsal rib to the posterior rim of the acetabulum.

Juvenile birds have, for a given trunk length, longer hindlimbs than their adult counterparts[20]; the same has been hypothesized for tyrannosaurids[21] and allosaurids[22]. Similarly, *Bambiraptor feinbergi*, a juvenile dromaeosaurid theropod, has a hindlimb/trunk length ratio of 2.0 (ref. 23) that is comparable to that seen in cursorial birds, but we exclude it from our analyses because of its obviously early stage of development. Additionally, *Sinornithoides youngi* was excluded from this study. The specimen also exhibits a bird-like hindlimb/trunk length ratio, is very small and possessed a cartilaginous sternum[24]. These observations indicate that this specimen, originally described as 'nearing maturity', may have been more immature than its describers supposed. To avoid confounding ontogenetic variables, the largest individual for each genus (for which we had data) was used in the analysis and data from known immature extant individuals were omitted as were extinct specimens whose maturity has in doubt.

The developmental maturity of *Caudipteryx* (NGMC 97–4–A and NGMC 97–9–A) is indicated by the well ossified sterna, sternal ribs, wrist bones and ankle bones[14]. Similar ossification is present in two more recently discovered, equivalently sized specimens, *Caudipteryx dongi* (IVPP V 12344)[25] and *Caudipteryx* (uncatalogued IVPP specimen) (Z. Zhou, personal communication), but the former specimen also possesses ossified uncinate processes. As these skeletal elements ossify late in development, there is little doubt that these individuals were mature.

Centre of mass calculations

Lateral and dorsal profiles of *Deinonychus* were compiled from reconstructions in ref. 19. Lateral and dorsal profiles of *Caudipteryx* were reconstructed from NGMC 97–4–A and NGMC 97–9–A. The axial body profiles were mathematically combined to create a solid three-dimensional model from which body volume and the location of centre of mass were calculated (see ref. 18 for details). The lung was conservatively assumed to have been spherical with a volume equal to 10% of body volume and positioned at the anterior portion of the trunk. The density of the lung ($0.4\,\mathrm{kg\,m^{-1}}$) was estimated using the ratio of mass-specific lung volume to mass-specific lung parenchyma volume in a large Nile crocodile[26].

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Genetic diversity and disease control in rice

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Crop heterogeneity is a possible solution to the vulnerability of monocultured crops to disease[1–3]. Both theory[4] and observation[2,3] indicate that genetic heterogeneity provides greater disease suppression when used over large areas, though experimental data are lacking. Here we report a unique cooperation among farmers,