fluviodeltaic origin by programmed-temperature closed-system pyrolysis. *Org. Geochem.* **26,** 467–481 (1997).
9. Pepper, A. S. & Dodd, T. A. Simple kinetic models of petroleum formation. Part II: Oil-gas cracking. *Mar. Petrol. Geol.* **12,** 321–340 (1995).
10. Price, L. C. Organic geochemistry of core samples from an ultra-deep hot well (300 °C, 7 km). *Chem. Geol.* **37,** 215–228 (1982).
11. Quigley, T. M. & McKenzie, A. S. The temperature of oil and gas formation in the subsurface. *Nature* **333,** 549–552 (1988).
12. Braun, R. L. & Burnham, A. K. PMOD: A flexible model of oil and gas generation, cracking and expulsion. *Org. Geochem.* **19,** 161–172 (1992).
13. Ungerer, P., Behar, F., Billalba, M., Heum, O. R. & Audibert, A. in *Advances in Organic Geochemistry 1987* (eds Mattavelli, L. & Novelli, L.) *Org. Geochem.* **13,** 857–868 (1988).
14. Price, L. C. Thermal stability of hydrocarbon in nature: Limits, evidence, characteristics and possible controls. *Geochim. Cosmochim. Acta* **57,** 3261–3280 (1993).
15. Petrov, A. A., Arefjev, O. A. & Yakubson, Z. V. in *Advances in Organic Geochemistry 1973* (eds Tissot, B. & Bienner, F.) 517–522 (Editions Technip, Paris, 1974).
16. Landa, S., Machacek, V., Mzourek & Landa *Chim. Ind.* (special no. 506) (1933) (in French).
17. Claypool, G. E. & Mancini, E. A. Geochemical relationships of petroleum in Mesozoic reservoirs to carbonate source rocks of Jurassic Smackover Formation, Southwestern Alabama. *Am. Assoc. Petrol. Geol. Bull.* **73,** 904–924 (1989).
18. Orr, W. Changes in sulfur content and isotopic ratios of sulfur during petroleum maturation—Study of Big Horn Basin Paleozoic oils. *Am. Assoc. Petrol. Geol. Bull.* **58,** 2295–2318 (1974).
19. Schleyer, P. A simple preparation of adamantane. *Am. Chem. Soc.* **79,** 3292 (1957).
20. Mello, M. R., Goncalves, F. T., Babinsky, N. A. & Miranda, F. P. Hydrocarbon migration and its near-surface expression. *Mem. Am. Assoc. Petrol. Geol.* **66,** 401–411 (1996).
21. Eglinton, G., Scott, P. M., Besky, T., Burlingame, A. L. & Calvin, M. Hydrocarbons of biological origin from a one-billion-year-old sediment. *Science* **145,** 263–264 (1964).
22. Eglinton, G. & Calvin, M. Chemical fossils. *Sci. Am.* **261,** 32–43 (1967).
23. Peters, K. E. & Moldowan, J. M. *The Biomarker Guide: Interpreting Molecular Fossils in Petroleum and Ancient Sediments* (Prentice Hall, Englewood Cliffs, NJ, 1993).
24. Summons, R. E., Powell, T. G. & Boreham, C. J. Petroleum geology and geochemistry of the Middle Proterozoic McArthur Basin, Northern Australia: III. Composition of extractable hydrocarbons. *Geochim. Cosmochim. Acta* **52,** 1747–1763 (1988).
25. Requejo, A. J. in *Biological Markers in Sediments and Petroleum* (eds Moldowan, J. M., Albrecht, P. & Philp, R. P.) 223–240 (Prentice Hall, Englewood Cliffs, NJ, 1992).
26. Thompson, K. F. M. Classification and thermal history of petroleum based on light hydrocarbons. *Geochim. Cosmochim. Acta* **47,** 303–316 (1983).
27. Sweeny, J. J. & Burnham, A. K. Evaluation of a simple model of vitrinite reflectance based on chemical kinetics. *Am. Assoc. Petrol. Geol. Bull.* **74,** 1559–1570 (1990).

Correspondence and requests for materials should be addressed to J.E.D. (e-mail: Dahl@Pangea.Stanford.edu).

Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya

H. Roche[*], A. Delagnes[*], J.-P. Brugal[†], C. Feibel[‡], M. Kibunjia[§], V. Mourre[‖] & P.-J. Texier[‖]

[*] *CNRS, Préhistoire et Technologie, MAE (boite 3), 21 allée de l'Université, 92023 Nanterre Cedex, France*
[†] *CNRS, UMR 6636, MMSH, 5 rue du Chateau de l'Horloge, 13094 Aix en Provence, France*
[‡] *Department of Anthropology, Rutgers University, New Brunswick, New Jersey 08903, USA*
[§] *National Museums of Kenya, PO Box 40658, Nairobi, Kenya*
[‖] *CNRS, Préhistoire et Technologie, CRA, Sophia Antipolis, 06565 Valbonne Cedex, France*

Well-documented Pliocene archaeological sites are exceptional. At present they are known only in East Africa, in the Hadar[1,2] and Shungura[3] formations of Ethiopia and in the Nachukui formation of Kenya. Intensive archeological survey and a series of test excavations conducted in the Nachukui formation since 1987 have led to the discovery of more than 25 archaeological sites whose ages range from 2.34 to 0.7 million years before present (Myr)[4,5], and to the extensive excavation of two 2.34-Myr sites, Lokalalei 1 in 1991 (refs 6, 7) and Lokalalei 2C in 1997. Lokalalei 2C yielded nearly 3,000 archaeological finds from a context of such good preservation that it was possible to reconstitute more than 60 sets of complementary matching stone artefacts. These refits, predating the Koobi Fora refits by 500 Kyr (ref. 8), are the oldest ever studied. Here we describe a technological analysis of the core reduction sequences, based on these refits, which allows unprecedented accuracy in the understanding of flake production processes. We can thus demonstrate greater cognitive capacity and motor skill than previously assumed for early hominids, and highlight the diversity of Pliocene technical behaviour.

Lokalalei 2C (LA2C; 3° 56′ 57.0″ N, 35° 46′ 43.7″ E) is situated in badlands exposures within the drainage of the Lokalalei sand bed ephemeral stream. The exposed sequence includes strata of the Lokalalei and Kalochoro members of the Nachukui formation[9] (Fig. 1). Near the site, both the Kokiselei and Ekalalei tuffs are exposed, and the archaeological site is 9 m above the latter (Fig. 2). Lokalalei 1 (ref. 9) is about 1 km away, at approximately the same stratigraphic level. A distinctive mollusc-packed sandstone 12 m below the sites is used for local correlation.

The Kokiselei tuff has been correlated with Tuff E of the Shungura formation[9], with a stratigraphically scaled age of 2.40 ± 0.05 Myr (ref. 10). The Ekalalei tuff is a geochemical correlate of Shungura tuff F-1 (ref. 9). This tuff lies immediately above Tuff F in the Omo (termed the Kalochoro tuff in West Turkana), which has been isotopically dated to 2.34 ± 0.04 Myr (ref. 10). The Ekalalei tuff (F-1) is thus slightly younger than 2.34 Myr, and is further constrained by an age of 2.32 Myr on Tuff G[11]. In the Shungura sections, Tuff G lies 30–45 m above Tuff F, and thus we can reasonably estimate an age of close to 2.34 ± 0.05 Myr for the Lokalalei archaeological sites.

The depositional sequence represented in the Lokalalei exposures includes a succession of fluvial facies separated by lacustrine deposits (Fig. 2), which probably correlate with the Lokeridede lake phase of the Turkana basin[12]. The Lokalalei sites are within floodplain paleosols in the upper fluvial strata, reflecting low energy, but proximal rather than distal, environments. LA2C is stratified in a clayey sand lens within a floodplain vertisol. The palaeogeographic setting of the site places it near the intersection of ephemeral basin-margin streams and the meandering, axial, ancestral Omo river.

A total of 17 m^2 was excavated at LA2C. The *in situ* material, comprising abundant artefacts and fewer faunal remains, formed a dense concentration (mean, 129 per m^2), with a very limited horizontal extension (10 m^2). It is vertically dispersed by up to 50 cm, largely by pedogenic churning of the associated vertic palaeosols. Despite this dispersion, the assemblage has remarkable archaeological homogeneity and preservation, which are demonstrated by the very fresh condition of the artefacts, the high proportion (28%) of small elements (<1 cm), the exceptional percentage of the refitted pieces (10% of the whole assemblage and 20% of the *in situ* material have been refitted) and the spatial distribution of refits, which corresponds closely with the distribution of the whole assemblage (Fig. 3).

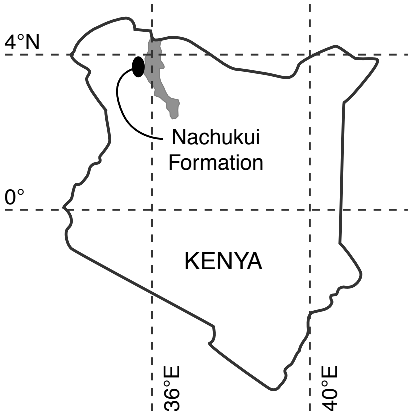

Figure 1 Map showing the location of the Nachukui formation.

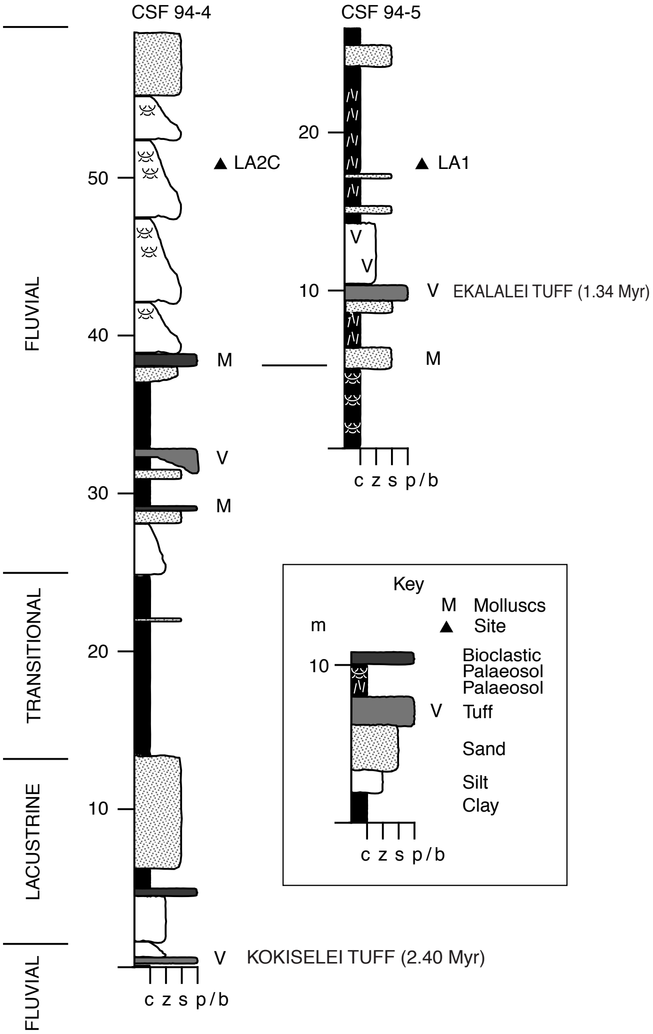

Figure 2 Stratigraphic sections through the Lokalalei archaeological sites. The sections represent the upper Lokalalei member and lower Kalochoro member, with the member boundary placed at about the level of the mollusc-packed sandstone, by which the two sections shown here are correlated. c, clay; z, silt; s, sand; p/b, pyroclastic or bioclastic sediment.

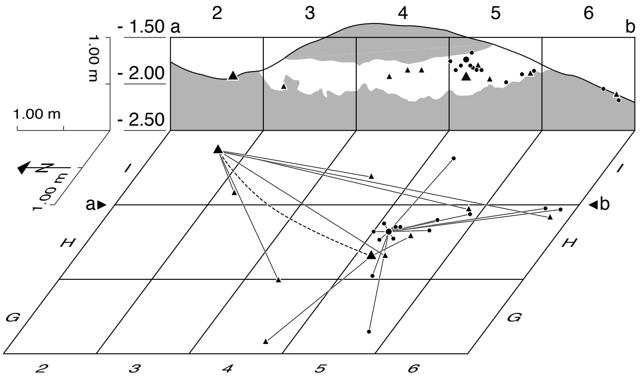

Figure 3 Horizontal and vertical distribution of R35 (triangles) and R9 (circles) refits. Three unplotted surface elements from R35 refit are not mapped. On the horizontal view, lines connect the flakes to their core. The dotted line joins two cores belonging to R35 refit, which were separately flaked after the block was broken. The arrowheads marked a and b indicate the horizontal axis along which the related vertical section was taken. G, H, I: west-east notation of grid squares; Numbers: north-south notation of grid squares.

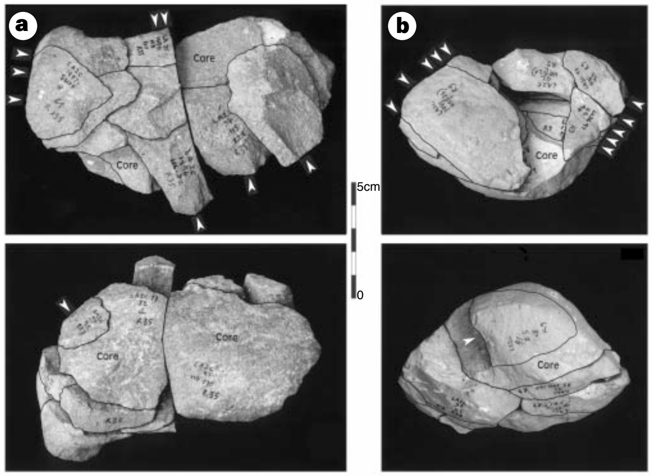

Figure 4 R35 and R9 refits. **a**, R35 refit (2 cores and 11 flakes). **b**, R9 refit (1 core and 14 flakes). These two refits are characteristic of the main reduction sequence: unidirectional or multidirectional removals flaked on a single debitage surface, from natural or prepared platforms. Arrows indicate the direction of the removals.

Table 1 Faunal remains (NISP) from LA2C

	Excavation	Surface	Total
Lamellibranches	1	1	2
Gasteropods	1		1
Fish (Siluriformes)	1	1	2
Cheloniens	19	8	27
Crocodylidae (*Crocodylus* sp.)	5	3	8
Reptile indet.	42	2	44
Aves (*Sthrutio* sp.)	17		17
Hystrix sp.		1	1
Bovid indet.	10		10
Bovid small	5	2	7
Bovid medium	3	3	6
Antilopini aff. *Gazella* sp.	2		2
Reduncini medium		2	2
Alcelaphini small	1	1	2
Hippotragini		1	1
Suid indet.		3	3
Kolpochoerus limnetes		1	1
Equid indet.		3	3
Hipparion aff. *ethiopicum*	2	1	3
Hippopotamid indet.		2	2
Ceratotherium sp.	9	1	10
Fragment indet.	99	109	208
Mammal large	2	4	6
Mammal indet.	22		22
Total	241	149	390

Faunal remains from LA2C represent 12 mammal species as well as various reptiles and fish. The excavation and surface zone yield, respectively, 241 and 149 faunal specimens (Table 1). Most of the material found *in situ* consisted of reptile bones, often fractured by compaction or pedogenesis. Shell fragments of a large land tortoise, together with several fragments of ostrich egg shell, are the best preserved elements of this relatively small faunal assemblage. Mammals are represented mainly by teeth and include bovids, suids, equids and a hyposodont rhinocerotid, attributed to *Ceratotherium simum germanoafricanum*. With the addition of this rhinocerotid and a large rodent (*Hystrix* sp.), the mammals from LA2C are characteristic of the species already recorded in the Kalochoro member[9]. They are essentially grazing species, indicating an open environment on an alluvial plain, with patches of bushes or forest along an ephemeral river. The fragmentation and the distribution of the fossils within the presumably short sequence of LA2C point to natural accumulation. The bones, which are encrusted and poorly preserved, show no evidence of anthropic action. However, the tortoise bones and ostrich-egg fragments are more closely associated with the lithic artefacts; their systematic presence in both Lokalalei sites may show a possible hominid collecting strategy.

The lithic assemblage from LA2C (Table 2) is dominated by debitage products (91%). These elements, associated with the cores and hammerstones, indicate that complete sequences (*chaînes opératoires*) of lithic production have taken place at the site. The rest of the assemblage consists of worked and unworked cobbles. The raw materials, mainly lavas (basalt and phonolite), were gathered from the ephemeral streams draining the Murua Rith range, which borders the Turkana basin on the west. Ten different categories have been identified, probably reflecting the diversity of raw materials available in the streams.

Study of the refitted material indicates that 60–70 cobbles were knapped on the spot to produce flakes (Table 2). Very few of these flakes were modified by subsequent retouching. Cores range from coarse-grained cobbles, from which only a few flakes have been removed, to cores of fine-grained lava pebbles, from which a large series of flakes (up to 30) have been produced. At LA2C, the dominant reduction sequence consists of these more reduced cores. Unidirectional or multidirectional removals are flaked on a single debitage surface, from natural or prepared platforms (Fig. 4). This knapping system allows the production of a long series of removals without changing the volumetric structure of the core. The repeated application by the knappers of the same technical principles to a whole series of cores, and during the reduction of each core, indicates an elaborate debitage scheme, implying motor precision and coordination. These principles include an appreciation of the quality of the collected raw materials, a judicious exploitation of the natural morphology of the blocks and the maintenance of adequate flaking angles during the entire debitage sequence. These show that the notion of production was already assimilated by a group of hominids in this particular area. This notion is integrated within a real debitage strategy, here well-mastered and unprecedented for this period.

Overall simplicity and similarities between assemblages are the two main arguments recently put forward to substantiate a technological stasis hypothesis between the 2.6 and 1.6 Myr time periods[2], and to merge the related assemblages into a single vast 'Oldowan' technocomplex. The stasis hypothesis cannot hold out against the detailed technological analysis of the LA2C lithic assemblage. There can be no doubt about the elaborate character of the LA2C debitage schemes, which are far more sophisticated than at any other Pliocene site. The assemblage also provides yet another example of the technical diversity within this time span. It should be stressed, however, that temporal variation is not necessarily in the direction of ever greater sophistication. Given the so-far largely underestimated spatio-temporal distance separating Plio-pleistocene 'Oldowan' assemblages[13], the variation observed probably reflects technical solutions to different environments and needs, as well as differences in cognitive and motor skills among early hominid groups characterized by non-synchronous evolutionary processes. ☐

Received 21 December 1998; accepted 19 March 1999.

Table 2 Composition of the lithic assemblage from LA2C

Category	Excavation	Surface	Total	Per cent of assemblage	Refitted	Per cent of category
Whole flakes	349	143	492	19.0	94	19.1
Broken flakes	491	260	751	29.1	95	12.6
Small flakes (< cm) and chips	690	27	717	27.8		
Fragments indet.	332	62	394	15.3	37	9.4
Retouched flakes	9	4	13	0.5	4	31
Whole cores	51	11	62	2.4	24	30.8
Broken cores	9	1	10	0.4	6	60.0
Chopper cores	1		1			
Tool cores	2	4	6			
Hammerstones	17		17	0.7		
Worked pebbles	16	2	18	0.7		
Broken pebbles	53	2	55	2.1	4	7.3
Unmodified pebbles	47		47	1.8		
Total	2,067	516	2,583	100.0	264	10.2

Of the 63 sets of refits which have been reconstituted, 50 sets comprise between 2 and 5 artefacts (51.8% of the refitted material), 9 sets between 6 and 10 artefacts, and the last 4 sets 11, 13, 15 and 20 artefacts, respectively. In 24 sets, the core is included. Some cobbles are totally or almost totally reconstructed (Fig. 4b). Other sets contain a large number of elements (for example, R33 refit, 20 elements) but are far from complete. Fragments indet.: non-orientable fragments.

1. Roche, H. & Tiercelin, J.-J. in *Proc. VIIth Panafrican Congress of Prehistory and Quaternary Studies* (eds Leakey, R. E. F. & Ogott, B.) 194–199 (Tilmiap, Nairobi, 1980).
2. Semaw, S. *et al.* 2.5-million-year-old stone tool from Gona, Ethiopia. *Nature* **385,** 333–336 (1997).
3. Howell, F. C., Heasaerts, P. & de Heinzelin, P. Depositional environment, archaeological occurrences and hominids from members E and F of Shungura Formation (Omo Basin, Ethiopia). *J. Hum. Evol.* **16,** 643–664 (1987).
4. Kibunjia, M., Roche, H., Brown, F. H. & Leakey, R. E. Pliocene and Pleistocene archaeological sites west of Lake Turkana, Kenya. *J. Hum. Evol.* **23,** 431–438 (1992).
5. Roche, H. & Kibunjia, M. Les sites archéologiques plio-pléistocènes de la Formation de Nachukui, West Turkana, Kenya. *Cr. Acad. Sc. Paris* **318,** 1145–1151 (1994).
6. Kibunjia, M. Pliocene archaeological occurrences in the lake Turkana Basin, Kenya. *J. Hum. Evol.* **27,** 157–171 (1994).
7. Kibunjia, M. *Archaeological Investigations of Lokalalei 1 (GaJh 5): A Late Pliocene Site, West of Lake Turkana, Kenya.* Thesis, Univ. Rutgers (1998).
8. Isaac, G. Ll. (ed.) *Koobi Fora Research Project* Vol. 5 (Clarendon, Oxford, 1997).
9. Harris, J. M., Brown, F. H. & Leakey, M. G. Stratigraphy and paleontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Contrib. Sci.* **399,** 1–128 (1988).
10. Feibel, C. S., Brown, F. H. & McDougall, I. Stratigraphic context of fossils hominids from the Omo Group deposits, Northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthropol.* **78,** 595–662 (1989).
11. Brown, F. H., McDougall, I., Davis, T. & Maier, R. in *Ancestors: The Hard Evidence* (ed. Delson, E.) 82–90 (Alan R. Liss, New York, 1985).
12. Feibel, C. S., Harris, J. M. & Brown, F. H. in *Koobi Fora Research Project* Vol. 3 (ed. Harris, J. M.) 321–370 (Clarendon, Oxford, 1991).
13. Roche, H. in *XIII° Int. Congress of Prehistoric and Protohistoric Sciences,* Colloquia Vol. 4, 55–63 (ABACO, Forlì, 1996).

Acknowledgements. We thank the Government of Kenya for permission to carry out this research and the National Museums of Kenya, Meave Leakey and the Kalokol Project for logistical support. The field work was funded by the French Foreign Affairs Ministry (Sous-Direction des Sciences Sociales, Humaines et de l'Archéologie). We thank Total (Kenya) for vehicles and fuel donation, and Crédit Agricole-Indosuez Bank for financial support. The team included J. Ekwiyeni, T. Harkaker, B. K. Kimeu, B. Kimolo, R. M. Kioko, B. Kyongo, E. Lokokodi, S. Mekwea, V. Mugao, K. S. Mulwa, D. Mutinda, A. Mutisya, S. Mutuku, A. Nares, L. K. Ngolokerem, T. Numbe and M. Twaha. We thank J. Feblot-Augustins for her help in translating and editing this paper.

Correspondence and requests for materials should be addressed to H.R. (e-mail: roche@mae.u-paris10.fr).

The wing of *Archaeopteryx* as a primary thrust generator

Phillip Burgers* & Luis M. Chiappe†

* *San Diego Natural History Museum, PO Box 121390, San Diego, California 92112, USA*

† *Vertebrate Paleontology, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, USA*

Since the late 1800s, the debate on the origin of flight in birds has centred around two antagonistic theories: the arboreal (take-off from trees) and cursorial (take-off from running) models[1–6]. Despite broad acceptance of the idea that birds evolved from bipedal and predominantly terrestrial maniraptoriform dinosaurs[1,7], the cursorial model of flight origins has been less successful than the arboreal model. Three issues have contributed to this lack of success: the gap between the estimated maximum running speed of *Archaeopteryx* (2 metres per second) and its estimated minimum flying speed (6 metres per second)[8]; the high energy demands of evolving flight against gravity[2,3]; and the problem of explaining the origin of the 'flight' stroke in an earthbound organism[3,4]. Here we analyse the take-off run of *Archaeopteryx* through lift-off from an aerodynamic perspective, and emphasize the importance of combining functional and aerodynamic considerations with those of phylogeny[1,9,10]. Our calculations provide a solution to the 'velocity gap' problem and shed light on how a running *Archaeopteryx* (or its cursorial maniraptoriform ancestors) could have achieved the velocity necessary to become airborne by flapping feathered wings.

Although, as a flier, it probably represents a relatively late stage in the evolution of bird flight, *Archaeopteryx* plays a central role in the debates on the origins of flight[2–6,11]. Proponents of the arboreal model consider *Archaeopteryx* to have been a tree climber, but evidence in support of this is weak at best[1,12–14]. Despite lacking the pulley-like action of the supracoracoid muscle of modern birds, which probably limited its capacity for carrying out fast, high-amplitude wing beats[15], *Archaeopteryx*'s pectoral musculature was apparently sufficient for flapping[16]. This conclusion is also supported by the lateral orientation of its glenoid facet[17] and the passive pronation-supination of its hand, as inferred from its wrist morphology[18]. Thus, *Archaeopteryx* appears to have been a predominantly terrestrial animal that, given the limited volume of its pectoral muscles and the relatively low amplitude of its wing beat, presumably had to run to take off [9,19], flapping its wings in a fashion similar to that of large extant birds[20].

Our aerodynamic model begins with *Archaeopteryx* initiating the take-off run with forward propulsion generated by its hindlimbs at the same time as it starts flapping its wings (Figs 1, 2). Calculations indicate that, during the take-off run, the initial hindlimb-supplied propulsion is gradually replaced by wing thrust (see Methods). Simultaneously, the lift generated by the wings—here called 'residual' as it does not exert work on the bird until lift-off—'unloads' the hindlimbs of the body weight (Fig. 2). This dual force migration (propulsion and body weight support) from the hindlimbs toward the wings has profound implications for the estimated maximum running speed of *Archaeopteryx*. Clearly, flapping increases the bird's running speed. As the residual lift due to flapping relieves the hindlimbs of body weight support, its running speed is further increased, which, in turn, increases the residual lift (which increases with the square of the running speed). At a certain point in the take-off run, the residual lift becomes greater than the bird's weight and so is converted to useful lift: *Archaeopteryx* takes off. At this point, lift becomes a force that exerts work on the bird. Wing thrust is now the sole source for generating the velocity necessary for sustained lift.

Previous calculations for the maximum running speed of *Archaeopteryx* assumed that its hindlimbs alone generated propulsive force and provided support for its full weight during the take-off run[8]. However, when the proposed upward force migrations are considered, *Archaeopteryx* can reach its estimated minimum flying speed (6 m s^{-1} in ref. 8), 7.8 m s^{-1} in our model) by means of the thrust and residual lift produced by its flapping wings. Our calculations indicate that, 3 s after beginning its take-off run, *Archaeopteryx* would have achieved a speed of 7.8 m s^{-1}. Extant lizards are known to have burst speeds which last for much longer times[21], and there is no indication that *Archaeopteryx* was metabolically incapable of the same. Thus, the 'velocity gap' ceases to exist.

This study indicates that *Archaeopteryx*'s wings may have been an efficient aerodynamic thrust generator. Although lift generation has been the focal point of most aerodynamic discussions on the origin of flight[22], the importance of thrust has often been underexplored. Thrust, however, must have played a fundamental role in the origin of flight. As shown in our calculations, thrust is the only force that exerts work on *Archaeopteryx* along its entire take-off run (residual lift does not exert any work). Thus, we regard thrust, and not lift, as the primordial force ultimately responsible for sustained flight. Because the direction of thrust is perpendicular to that of gravity, not against it, objections to the cursorial theory on the basis of strenuous energetic demands[2] may not be relevant.

Even though our study centres on *Archaeopteryx*, our conclusions can be applied equally to non-avian maniraptoriforms flapping their wings in a downstroke–upstroke fashion. It is likely that these dinosaurs had the ability to passively supinate and flex their forelimbs[9,18] as well as to flap them within ranges comparable to those of *Archaeopteryx*[9,23]. Some of them have even been found to possess fully fledged wings[24]. Thus, the structures and functions necessary for wing-generated thrust were already present in the flightless ancestors of birds. Long, vaned feathers, like those of the non-avian theropods *Caudipteryx* and *Protarchaeopteryx*[24], and the 'flight' stroke evolved in the context of terrestrial thrust. As previously implied[25,26], wing-generated thrust evolved before useful lift. Using this thrust and its ensuing residual lift, the flightless