

Early Adaptive Radiation of Birds: Evidence from Fossils from Northeastern China

Lianhai Hou, Larry D. Martin, Zhonghe Zhou, Alan Feduccia*

Late Jurassic and Early Cretaceous birds from northeastern China, including many complete skeletons of *Confuciusornis*, provide evidence for a fundamental dichotomy in the class Aves that may antedate the temporal occurrence of the Late Jurassic *Archaeopteryx*. The abundance of *Confuciusornis* may provide evidence of avian social behavior. Jurassic skeletal remains of an ornithurine bird lend further support to the idea of an early separation of the line that gave rise to modern birds. *Chaoyangia*, an ornithurine bird from the Early Cretaceous of China, has premaxillary teeth.

The recent discovery of numerous Early and Late Cretaceous birds from Europe, Asia, South and North America, and Australia (1, 2) has led to the discovery that the enantiornithine or "opposite" birds were the dominant landbirds of Cretaceous ecosystems (3). These birds differ from modern, ornithurine birds most prominently in the proximodistal direction of fusion of the metatarsal bones and in a different conformation of bones forming the triosseal canal for the flight apparatus (1-3). Modern ornithurine birds are now also known from the Early Cretaceous, including the Mongolian *Ambiortus* (4) and the Chinese *Gansus* (5) and *Chaoyangia* (6). Hesperornithiform birds were already well specialized for foot-propelled diving by the latter part of the Early Cretaceous (Aptian), and their divergence from other ornithurine birds must have been quite early (7). All of the previous work on the early radiation of birds has been largely superseded by many nearly complete specimens recently discovered in the Jurassic-Cretaceous deposits of northeastern China. Here, we report on three of the most critical taxa from this region in terms of stratigraphic position, phylogenetic implications, and completeness.

Confuciusornis was described from three partial skeletons (8), but Chinese workers have discovered many new and complete specimens (Fig. 1) that show almost all aspects of the skeletal anatomy and much of the plumage. We have revised our original restoration (8) on the basis of this new material (Fig. 2B). The pelvis and the climbing adaptations in the hands indicate

a vertical, *Archaeopteryx*-like posture (Fig. 2A). The foot of *Confuciusornis* is similar to *Archaeopteryx*, with a reflexed hallux and large recurved pedal claws reflecting an arboreal life-style. The metatarsals are fused proximally but not distally, and a distinct

fifth metatarsal is present (Fig. 2D). A small unkeeled sternum, much like that of the seventh *Archaeopteryx*, is present and lies at the front of a well-developed series of gastralia (Figs. 1D and 2B). The coracoid is more elongate than in *Archaeopteryx* and seems to articulate on the anterior margin of the sternum. There is a broad *Archaeopteryx*-like furcula. The bony tail is short, and in some specimens the bones fuse distally to form a long pygostyle (eight vertebrae). The number of free caudals after the formation of the pygostyle seems to be very small (perhaps four to five). The variability in pygostyle formation may result from ontogeny or may reflect differences in the stratigraphic position of the specimens. The absence of teeth is confirmed in the seven new specimens with skulls. The plumage can in part be restored and shows a long feathered tail and a well-developed wing with asymmetric remiges, indicating volant

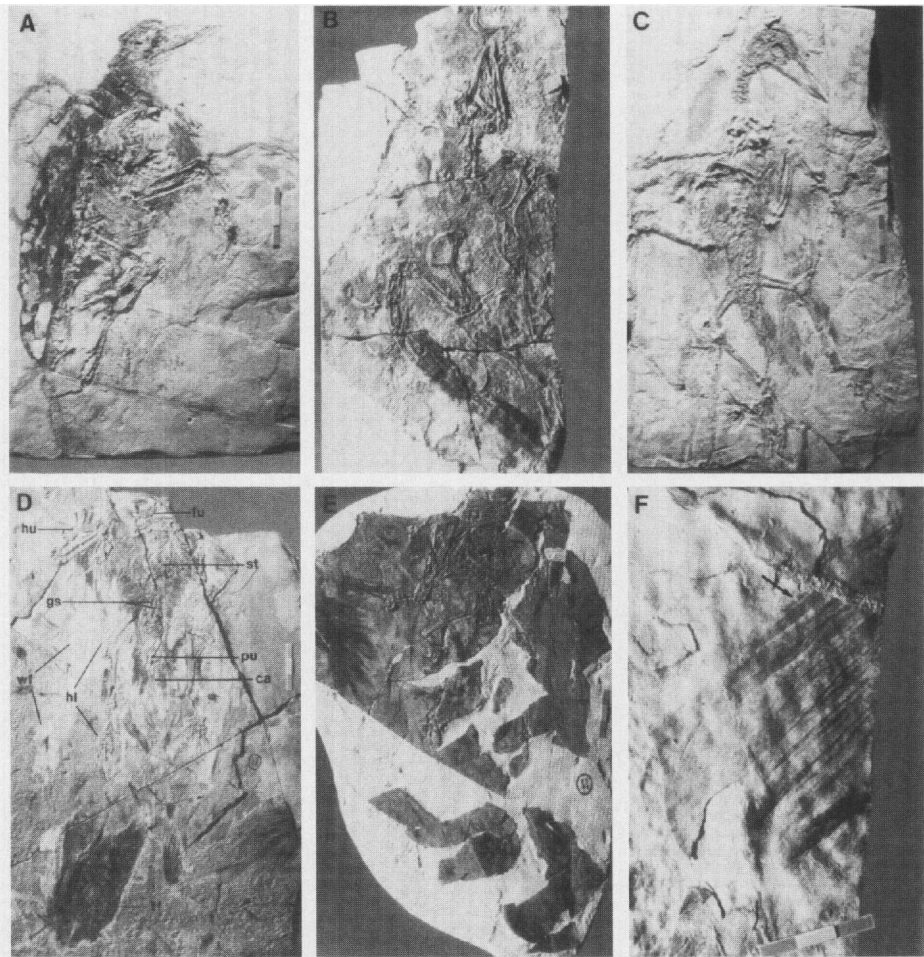


Fig. 1. New specimens of the primitive bird *Confuciusornis sanctus* in the collections of IVPP in Beijing, China. (A to C) Skeletons with skulls and jaws [(C), skull restored by collector]; (B) shows primaries of right wing, and (C) shows tail vertebrae in ventral view. (D and E) Slab and counterslab, showing the outline of the tail and wing feathers, *Archaeopteryx*-like reflected pubis, but shortened skeletal tail. Abbreviations in (D): hu, humerus; fu, furcula; st, sternum; gs, gastralia; pu, pubis; ca, caudal skeleton; wf, wing feathers; hl, hindlimbs; and tf, tail feathers. (F) Strongly asymmetric remiges. Total length of scale bars, 3 cm.

L. Hou, Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Post Office Box 643, Beijing 100044, China.
L. D. Martin, Natural History Museum, University of Kansas, Lawrence, KS 66045, USA.
Z. Zhou, IVPP, Chinese Academy of Sciences, Post Office Box 643, Beijing 100044, China, and Natural History Museum, University of Kansas, Lawrence, KS 66045, USA.
A. Feduccia, Department of Biology, University of North Carolina, Chapel Hill, NC 27514, USA.
*To whom correspondence should be addressed.

ability. There are indications of a full-body covering of contour feathers. The general outline of the feathered tail, although formed in a different manner from that of *Archaeopteryx* (which has a long reptilian series of caudal vertebrae), is quite similar in form to that of the Solnhofen bird. It is long and broad in silhouette and is not dissimilar to that of the magpie (*Corvidae*) or coucal (*Cuculidae*).

The same deposits that produced *Confuciusornis* yielded a partial skeleton of a bird, *Liaoningornis* (9) (Fig. 2C) with a keeled sternum, which constitutes the earliest evidence for this distinctly avian structure. The keel extends nearly to the front of the sternum and there are coracoidal sulci. The sternal end of the coracoid is extended medially and there is a sternocoracoidal process. The xiphial end of the sternum is expanded laterally, and the sternal notch is indented. All of these are ornithurine bird features, as is the fusion of the distal end of the tarsometatarsus but not the proximal end, with the proximal end covered by a tarsal cap. The sternum is long and broad so that it could act as a pump for the air sacs. Because enantiornithine birds did not have the ornithurines' long posterior abdominal extension of the sternum, they would have lacked the capacity for higher rates of oxygen consumption during flight and therefore would not have had a modern avian-style flow-through lung. Uncinate processes hinging on the rib cage are found in all ornithurine birds but not in *Archaeopteryx*, *Confuciusornis*, or any enantiornithine bird. This argues for modern air-sac breathing in ornithurine birds but against it in all sau- rian birds, including *Archaeopteryx*, as

they would be unable to ventilate the abdominal air-sac system (10). Recent histological work shows that the Late Cretaceous enantiornithines lacked endothermy (11). These fundamental anatomical differences between the two major avian groups indicate that the early avian dichotomy was characterized not only by divergent locomotory architecture but also by thermoregulatory and activity physiology. *Liaoningornis* has sharp recurved claws and probably spent much of the time in trees; such an interpretation is also supported by its broad, short tarsometatarsus (proportioned much like that of *Coraciiformes*) and large reflexed hallux. The femur is long (about the length of the tibiotarsus) and the fibula nearly reaches the ankle.

The next oldest ornithurine bird is *Chaoyangia* from the Early Cretaceous of China. *Chaoyangia* was originally described from a vertebral column, ribs, pelvis, femur, and tibiotarsus (6). Since then, the same complex of deposits has produced a partial foot and a shoulder girdle including the furcula, coracoids, and sternum. Although there is little skeletal overlap among these specimens, they are from birds of nearly the same size and are the only ornithurine material present in deposits that have produced more than 25 specimens of enantiornithine birds. One of the new specimens of *Chaoyangia* shows a toothed dentary and premaxillary as well as other fragmentary skull parts. These show the typical tooth morphology found in *Parahesperornis*, *Hesperornis*, *Ichthyornis*, *Archaeopteryx*, and *Cathayornis*. The shoulder girdle is similar to that of *Ambiortus*, and both *Chaoyangia* and *Ambiortus* have coracoids with deep, round scapular facets

and long straplike procoracoidal processes (Fig. 3A) that readily separate them from the enantiornithines. Both genera also resemble each other and differ from the shoulder girdle of enantiornithines (Fig. 3B) in that (i) the furcular arms are rounded and internally flexible; (ii) the furcular hypocleidium is undeveloped (enormously enlarged in enantiornithines); (iii) the sternum is elongated and not greatly emarginated posteriorly as in enantiornithines; (iv) the coracoidal facets are posterior to the anterior margin of the sternum (on that margin in enantiornithines); and (v) the sternal keel reaches almost to the anterior margin of the sternum (much posterior to the anterior margin in enantiornithines).

These fossils show that the scapula and coracoid characters first used to distinguish Enantiornithes (1, 2) were already well established by the Early Cretaceous. The finding of such extensive differences at such an early date does not support a lineal evolutionary scenario in which *Archaeopteryx* is an ancestor to all later birds and the enantiornithines are an intermediate stage on the way to modern birds, as suggested by Chiappe (1). What is documented is an independent improvement of flight-related morphology from a common ancestor somewhat less specialized than *Archaeopteryx*. The ossification of the cartilaginous sternum, development of a sternal keel, and elongation of the coracoids were evidently developed in parallel, thus accounting for the differences in the systems used by ornithurine and enantiornithine birds to achieve the same purposes.

The Early Cretaceous enantiornithine bird *Cathayornis* has an *Archaeopteryx*-like

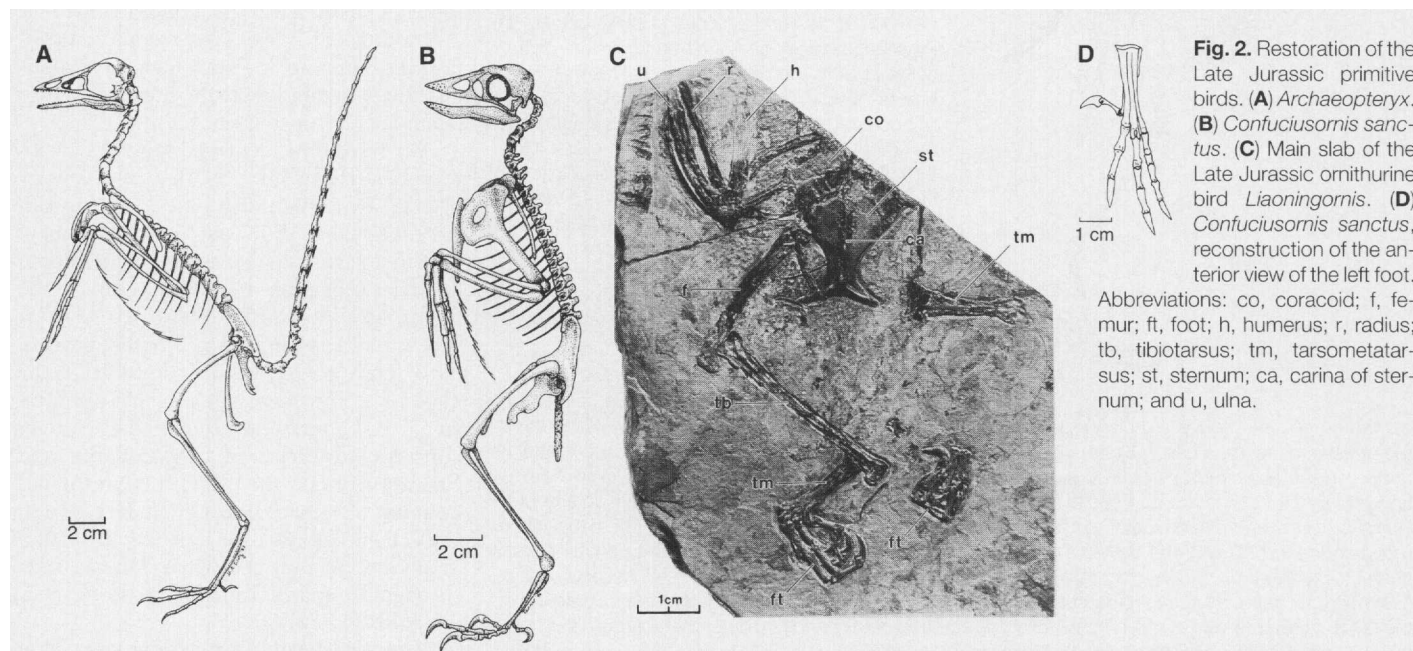


Fig. 2. Restoration of the Late Jurassic primitive birds. (A) *Archaeopteryx*. (B) *Confuciusornis sanctus*. (C) Main slab of the Late Jurassic ornithurine bird *Liaoningornis*. (D) *Confuciusornis sanctus*, reconstruction of the anterior view of the left foot.

Abbreviations: co, coracoid; f, femur; ft, foot; h, humerus; r, radius; tb, tibiotarsus; tm, tarsometatarsus; st, sternum; ca, carina of sternum; and u, ulna.

skull with the nasals meeting in the midline and toothed premaxillaries. These primitive cranial features are coupled with an outer metacarpal extending distally beyond the middle metacarpal (12), a derived feature characteristic of the enantiornithiforms (1, 2). This condition is uncertain in *Gobipteryx* (13), although a newly collected specimen as well as the known embryos of *Gobipteryx* suggest that a primitive metacarpal position (middle and outer at about the same level) may be present. If this is so, then *Gobipteryx* may be a side branch of enantiornithine evolution united by the development of a horny bill with *Confuciusornis* of the Jurassic-Cretaceous transition (8).

By combining all the putative specimens of *Chaoyangia*, we can reconstruct an Early Cretaceous ornithurine bird (Fig. 3C). This bird was adapted for wading and had small pedal claws, a large rib cage, and a basically modern shoulder girdle. The Early Cretaceous ornithurine bird *Ambiortus* differs from modern birds in having two well-developed wing phalanges and a claw on the second digit. This probably was also the case in *Chaoyangia*, although only the finger of the third digit is known, but this digit also had a small claw.

The Late "Jurassic" Chinese bird *Confuciusornis* illustrates the early evolution of a horny or keratinized beak and edentulous

jaw, as well as the advent of a prokinetic skull. *Confuciusornis* illustrates a rapid transition to a partially modern cranial morphology in one line, whereas other Mesozoic birds retained more primitive toothed jaws but developed a more advanced flight morphology. The Chinese fossils, unlike *Archaeopteryx* (from deposits laid down in a hypersaline lagoon in Germany), are from inland lacustrine deposits that have also yielded numerous freshwater fossils, including fish, ostracods, and conchostracians. The large number of new specimens of *Confuciusornis sanctus* from a small area is so exceptional as to suggest some sort of communal life-style for this species, and the size range of individuals may be indicative of indeterminate growth.

The small, sparrow-sized Early Cretaceous birds from Spain (14) now include four genera—*Iberomesornis*, *Concornis*, *Noguerornis*, and *Eoalulavis*—that are morphologically similar and might represent a single genus (only minor diversification). These are all known from deposits that are of lacustrine or lagoonal origin but are preserved in limestones of the same general type as were deposited in the Late Jurassic of Solnhofen. In recent years it has become apparent that the Spanish fossils belong to the enantiornithine birds, and a diverse variety of these birds are now known from localities that include Asia, Australia, and North and South America (1, 2, 15). Enantiornithine birds from the Chinese Lower Cretaceous (12, 16) now come from some seven localities with more than 30 individuals falling into three or more major morphological types, including *Sinornis* (17), *Cathayornis* (18), and *Boluochia* (19). In addition, *Chaoyangia*, an ornithurine bird, occurs in the same deposits with the enantiornithines. An additional Lower Cretaceous ornithurine bird, *Gansus* (5) with its long phalanges and elongated fourth toe, probably also occupied the near-shore habitat.

We have now identified several synapomorphies (Fig. 3D) (20) that ally *Archaeopteryx* with enantiornithine birds, including proximal-to-distal ontogenetic fusion of the metatarsal elements, a posterolateral condylar ridge on the distal end of the femur, an anteromedially directed scapular process, and an anterodorsal ischial process. This lends credence to a division of the class Aves into two major subclasses, Sauriurae (21) and Ornithurae. The former contains *Archaeopteryx*, *Confuciusornis*, and *Enantiornithes*; the latter (Ornithurae) contains all other known birds. In contrast, the scheme of Chiappe indicates an orthogenetic lineage that goes from *Archaeopteryx* through an enantiornithine grade to modern birds (1, 22).

The new fossils from China show that

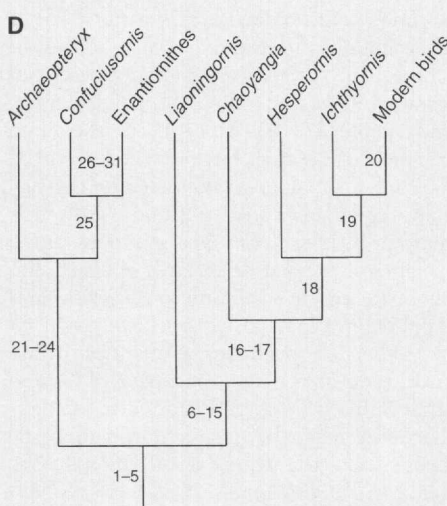
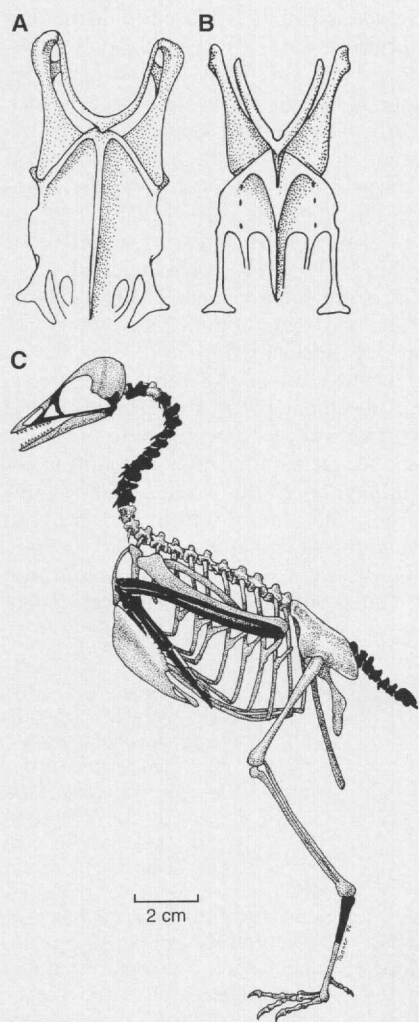


Fig. 3. Restoration of the shoulder girdle (coracoids, furcula, and sternum) of (A) *Chaoyangia* and (B) *Confuciusornis* from a ventral view. (C) Reconstruction of the *Chaoyangia* skeleton; the wing and neck are based on *Ambiortus* and the tail on *Ichthyornis* (restorations are in solid black). (D) Phylogenetic relations of some important genera of Mesozoic birds (20). Derived characters of each group: Aves is diagnosed by (1) feathers, (2) loss of postorbital bone, (3) posterior pubic spoon, (4) opisthopubic pelvis, and (5) reflexed hallux. Ornithurae are diagnosed by (6) laterally flexible furcula, (7) rounded concave scapular facet on the coracoid, (8) distinct straplike procoracoidal process, (9) keel almost reaching anterior margin of sternum, (10) sternum elongated and reaching the abdominal region, (11) sternum with coracoidal sulci, (12) uncinat processes on ribs, (13) distal-to-proximal metatarsal fusion, (14) fusion of the distal ends of the outer two metacarpals, and (15) tarsal cap on the tarsometatarsus. Other un-

named ornithurine groups are diagnosed by (16) small pedal claws, (17) proximal fusion of the tarsometatarsus to the tarsal cap, (18) separation of the distal pubes, (19) hypotarsus, and (20) supratendinal bridge on the tibiotarsus. Sauriurae is diagnosed by (21) broad furcular arms that are grooved posterodorsally (laterally noncompressible), (22) outer condyle of femur with a dorsal crest, (23) anterodorsal ischial process, and (24) proximal-to-distal metatarsal fusion. *Confuciusornis* and *Enantiornithes* share (25) a shortened tail with the development of a pygostyle, and distinct pleurocoels. *Enantiornithes* is characterized by (26) reduced fingers, (27) elongated coracoid with a nonterminal raised scapular facet, (28) triangular depression on the dorsal surface of the coracoid, (29) greatly elongated hypocleidium on the furcula, (30) sternal keel much posterior to the anterior margin, and (31) outer metacarpal distal to the others. See (1) for a contrasting view of Mesozoic bird evolution.

the two major clades of avian evolution, the Sauriurae and the Ornithurae, were sympatric only a few million years after the occurrence of *Archaeopteryx*. By the Jurassic-Cretaceous transition, birds had already undergone a remarkable and probably rapid radiation. The new information on the early geographic and temporal distribution of birds may also indicate a long avian history in the Jurassic. We would expect that the common ancestor of the Sauriurae and the Ornithurae would pre-date *Archaeopteryx* and that we may reasonably search for birds in Middle Jurassic and older beds. This exacerbates one of the most obvious conundrums facing the theory of a dinosaurian origin of birds. The dinosaurs thought to be most like birds are primarily Late Cretaceous in age and are younger than *Archaeopteryx* by more than 76 million years. This temporal paradox has led some dinosaur experts to argue that birds gave rise to certain late Cretaceous theropods (23).

The dating of the Jurassic-Cretaceous boundary remains controversial in north-eastern China (8). We have accepted an age for *Confuciusornis* and *Liaoningornis* somewhat younger than *Archaeopteryx* but still older than any other known birds, and we think that these deposits essentially bridge the Jurassic-Cretaceous transition. Any more precise dating will require further field work in China.

REFERENCES AND NOTES

1. L. M. Chiappe, *Nature* **378**, 349 (1995).
2. L. D. Martin, *Cour. Forschungsinst. Senckenb.* **181**, 25 (1995); C. A. Walker, *Nature* **292**, 51 (1981).
3. A. Feduccia, *Science* **267**, 637 (1995).
4. E. N. Kurochkin, *Cretaceous Res.* **6**, 272 (1985).
5. L. Hou, *Sci. Sin. Ser. B* **27**, 1296 (1984).
6. L. Hou and J. Zhang, *Vertebr. Palasiat.* **31**, 217 (1993).
7. L. D. Martin, in *Perspectives in Ornithology*, A. H. Brush and G. A. Clark Jr., Eds. (Cambridge Univ. Press, New York, 1983), pp. 291–338.
8. L. Hou, Z. Zhou, Y. Gu, H. Zhang, *Chin. Sci. Bull.* **40**, 1546 (1995); L. Hou, Z. Zhou, L. D. Martin, A. Feduccia, *Nature* **377**, 616 (1995).
9. L. Hou, *Chin. Sci. Bull.*, in press.
10. J. Ruben, personal communication.
11. A. Chinsamy, L. M. Chiappe, P. Dodson, *Nature* **368**, 196 (1994).
12. Z. Zhou, *Cour. Forschungsinst. Senckenb.* **181**, 9 (1995).
13. A. Elzanowski, *Nature* **264**, 51 (1976); *Palaeontol. Pol.* **42**, 147 (1981).
14. J. L. Sanz, J. F. Bonaparte, A. Lacasa, *Nature* **331**, 433 (1988); J. L. Sanz and A. D. Buscalioni, *Paleontology* **35**, 829 (1992); A. Lacasa, *Estud. Geol.* **45**, 417 (1989); J. L. Sanz, L. M. Chiappe, A. D. Buscalioni, *Am. Mus. Novit.* **3133**, 1 (1995); J. L. Sanz et al., *Nature* **382**, 442 (1996).
15. L. M. Chiappe, *Am. Mus. Novit.* **3083**, 1 (1993).
16. Z. Dong, *Can. J. Earth Sci.* **30**, 2177 (1993).
17. P. C. Sereno and Rao Chenggang, *Science* **255**, 845 (1992).
18. Z. Zhou, F. Jin, J. Zhang, *Chin. Sci. Bull.* **37**, 1365 (1992).
19. Z. Zhou, *Vertebr. Palasiat.* **33**, 99 (1995).
20. The data matrix and PAUP analysis are available at Science's Beyond the Printed Page site on the World Wide Web: <http://www.sciencemag.org/science/feature/data/hou.shl>
21. E. N. Kurochkin, special issue of the Palaeontological Institute of the Russian Academy of Sciences, Moscow (1996).
22. L. M. Chiappe, in *Contribution of South America to Vertebrate Paleontology*, G. Arratia, Ed., *Muenchener Geowiss. Abh.* **A30**, 203 (1996).
23. G. Paul, *Predatory Dinosaurs of the World* (Simon and Schuster, New York, 1988).
24. We thank J. Chorn and D. Miao for reading the manuscript, C. Bennett for helpful suggestions, and the Chinese Natural Science Foundation and the National Geographic Society (U.S.) for support for fieldwork. Zhang Jie and S. Whitfield kindly helped prepare the figures; the drawings are by M. Tanner and M. A. Klotz.

17 July 1996; accepted 24 September 1996

Direct Observation of Vortex Dynamics in Superconducting Films with Regular Arrays of Defects

K. Harada, O. Kamimura, H. Kasai, T. Matsuda, A. Tonomura, V. V. Moshchalkov

The microscopic mechanism of the matching effect in a superconductor, which manifested itself as the production of peaks or cusps in the critical current at specific values of the applied magnetic field, was investigated with Lorentz microscopy to allow direct observation of the behavior of vortices in a niobium thin film having a regular array of artificial defects. Vortices were observed to form regular and consequently rigid lattices at the matching magnetic field, at its multiples, and at its fractions. The dynamic observation furthermore revealed that vortices were most difficult to move at the matching field, whereas excess vortices moved easily.

Many efforts have been made to increase the critical current density J_c of superconductors by introducing defects as pinning centers into superconductors. A high J_c , the maximum current density at which these defects can still pin down vortices against the Lorentz force exerted on vortices by a current, can be obtained when the elementary pinning force of individual pinning centers is strong.

However, the pinning effect cannot be estimated without taking the whole behavior of vortices into consideration. In fact, J_c has peak values at specific applied magnetic fields H (1, 2). This "matching effect" has been attributed to the commensurability between arrays of vortices and defects: J_c (3) and the magnetization M (4–6) measured for superconductors with a regular array of artificial defects had peaks or cusps at specific H values, or "matching fields" $H = H_n$. The H values corresponded to the cases where the occupation number n of vortices at defects was an integer or its fractions. Hence, indirectly, the increase in J_c was related to the formation of regular and rigid vortex lattices assisted by the existence of defects.

In the present experiment, the static and dynamic behaviors of individual vortices

were directly observed in superconducting thin films with a square array of artificial defects, in order to elucidate the microscopic mechanism of the matching effect. The simultaneous static observation of both vortices and defects that is necessary for such experiments has been made only for special cases with Bitter techniques (7–9) and scanning probe microscopy (10, 11). At the same time, Lorentz microscopy (12) and electron holography (13) using a 300-kV field emission electron microscope have opened a way for simultaneous observation of both vortices and defects, not only statically but also dynamically. This has made it feasible to investigate the dynamic interaction of vortices with pinning centers (14, 15). The present experiment was carried out with Lorentz microscopy.

The experimental procedure was as follows. A Nb thin-film sample was prepared by chemically etching 15- μm -thick foil that had been annealed at 2200°C for 10 min to increase its grain sizes up to ~ 300 μm in diameter. The film had one or more holes in the central part. In peripheral regions in the film that were < 100 nm thick near the holes, a square array of 13 by 13 small defects was produced inside a region 10 μm by 10 μm (defect spacing $d = 0.83$ μm) by irradiation of the Nb film with a focused 30-kV Ga^+ ion beam from a Hitachi focused ion beam machine (FB-2000). The defect consisted of a pit 30 nm in diameter and a few nanometers in depth, and of dislocation networks 200 nm in di-

K. Harada, O. Kamimura, H. Kasai, T. Matsuda, A. Tonomura, Advanced Research Laboratory, Hitachi, Ltd., Hatoyama, Saitama 350-03, Japan.
V. V. Moshchalkov, Laboratorium voor Vaste-Stoffysica en Magnetisme, Katholieke Universiteit Leuven, B-3001 Leuven, Belgium.