clones reflected the character of the particular clone and the number of cells on the plate from which the virions were obtained.
19. L. Sealy, M. L. Privalsky, G. Moscovici, C. Moscovici, J. M. Bishop, *Virology* **130**, 155 (1983).
20. D. E. Schwartz, R. Tizard, W. Gilbert, *Cell* 32, 853 (1983).
21. S. Kawai and M. Nishizawa, *Mol. Cell. Biol.* **4**, 1172 (1984).
22. M. Frohman, in *PCR Protocols. A Guide to Methods and Applications*, M. Innis, D. Gelfand, J. Sninsky, T. White, Eds. (Academic Press, New York, 1990), p. 28.
23. S. Goff, P. Traktman, D. Baltimore, *J. Virol.* **38**, 239 (1981).
24. T. Maniatis, E. F. Fritsch, J. Sambrook, *Molecular Cloning: A Laboratory Manual* (Cold Spring Harbor Laboratory, Cold Spring Harbor, NY, 1982).
25. We thank N. Rosenberg and T. Stacy for discussion, S. Dobson for technical assistance, and C. Moore for the pT 3L3 plasmid. Supported by research grant R35 CA 44385 from the National Cancer Institute.

12 June 1991; accepted 4 November 1991

Early Evolution of Avian Flight and Perching: New Evidence from the Lower Cretaceous of China

PAUL C. SERENO* AND RAO CHENGGANG

Fossil bird skeletons discovered in Lower Cretaceous lake deposits in China shed new light on the early evolution of avian flight and perching. The 135 million-year-old sparrow-sized skeletons represent a new avian, *Sinornis santensis*, n. gen. n. sp., that preserves striking primitive features such as a flexible manus with unguals, a footed pubis, and stomach ribs (gastralia). In contrast to *Archaeopteryx*, however, *Sinornis* exhibits advanced features such as a broad sternum, wing-folding mechanism, pygostyle, and large fully reversed hallux. Modern avian flight function and perching capability, therefore, must have evolved in small-bodied birds in inland habitats not long after *Archaeopteryx*.

THE SKELETON OF THE OLDEST BIRD, *Archaeopteryx*, is characterized by elongate grasping forelimbs and a long balancing tail, and its skeleton resembles in many regards that of its nearest theropod relatives (*1*). *Archaeopteryx*, nevertheless, was clearly capable of gliding or primitive powered flight, as evidenced by flight feathers of modern avian aerodynamic design and arrangement along the forearm and manus (*2*). Late Cretaceous carinate birds such as *Ichthyornis*, in contrast, exhibit an advanced avian flight apparatus, including an expansive keeled sternum for bulky flight musculature and wing and tail modifications for aerial maneuverability (*3*). The basic components of the modern avian flight apparatus, thus, must have arisen in the Early Cretaceous, during the first third of avian history.

But the fossil record for the Early Cretaceous, thus far, has provided little documentation of this critical transformation (*4*). Recently, partial bird skeletons have been discovered in the Lower Cretaceous of Asia (*5*) and Europe (*6*) (Fig. 1) that provide important clues to the early evolution of flight, but none of these specimens is complete. We report on the discovery of sparrow-sized bird skeletons in Lower Cretaceous beds in northeastern China (*7*). The holotype skeleton (Fig. 2B) of the new bird, *Sinornis santensis*, n. gen. n. sp. (*8*), is preserved on part and counterpart slabs of fine-grained freshwater lake sediment and is associated with abundant fish (*Lycoptera*), insect, and plant remains (*9*). The associated pollen and spore assemblage suggests a Valanginian age for the bird (*10*), which, if correct, would make it second only to *Archaeopteryx* in age among birds (Fig. 1C).

The skull and skeleton exhibit a number of striking primitive features that have not been reported thus far in any bird except *Archaeopteryx*. The skull has a proportionately short, toothed snout (Fig. 2A) as in *Archaeopteryx*. The carpus and manus in the forelimb are separate, rather than fused into a unit carpometacarpus, and the manus is composed of freely articulating metacarpals, with well-formed phalanges and unguals on the first and second digits (Fig. 3C). The manual unguals are relatively small and only moderately recurved, in contrast to the slender, highly recurved unguals in *Archaeopteryx* (*11, 12*). The pelvis is remarkably primitive and closely resembles that of *Archaeopteryx* (Fig. 4B). The elements of the pelvic girdle are free rather than coossified (*6, 12*), the iliac blades are erect rather than converging toward the midline, and the ischium is blade-shaped rather than strap-shaped. The rodlike shaft of the pubis appears to be directed more ventrally than posteriorly and terminates distally in a hook-shaped foot similar to that in *Archaeopteryx* and theropod dinosaurs. As in *Archaeopteryx*, the metatarsals are separate, rather than coossified, along all but their proximal ends. Rows of slender stomach ribs (gastralia) are preserved on the ventral aspect of the trunk, passing between the hind limbs (Fig. 4B). Gastralia have been lost in all other birds except *Archaeopteryx* (*12*). These retained archaic features are not specifically involved in flight or perching and add to current evidence that favors theropod dinosaurs as the nearest avian relatives. Lack of fusion in the manus, pelvis, and hind limbs seems to document the primitive avian condition, rather than signify immaturity in the holotype skeleton, because bone surfaces are finished throughout the skeleton and the components in the dorsal vertebrae and pygostyle are completely fused (*13*).

Advanced avian characters in the skeleton of *Sinornis* are almost all directly related to flight or perching. There appear to be no more than 11 dorsal vertebrae in the trunk as in the Spanish bird (*6*), rather than 14 as occur in *Archaeopteryx* and most theropods. The tail is short with only eight free vertebrae and a large pygostyle for attachment of the rectricial fan. The short trunk and tail in *Sinornis* shift the center of mass toward the forelimbs, as in modern powered fliers, as opposed to a center of mass near the hind limbs, as in the terrestrial cursor *Archaeopteryx*. In living birds the pygostyle is closely correlated with the size of the rectricial fan

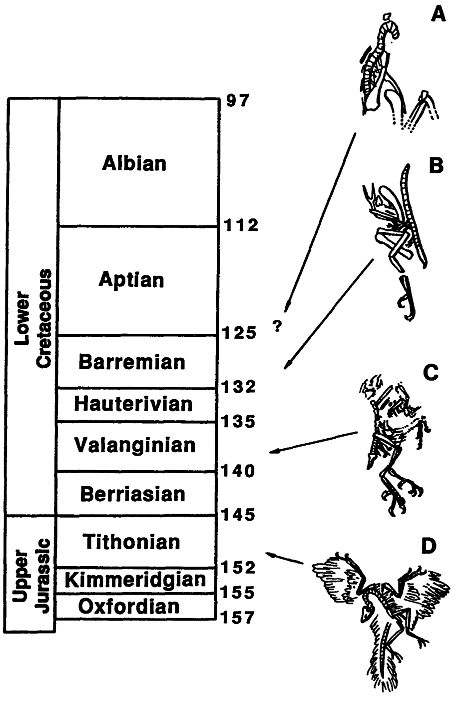


Fig. 1. Temporal position of Upper Jurassic and Lower Cretaceous fossil birds. (**A**) *Ambiortus dementjevi*, (**B**) Las Hoyas bird, (**C**) *Sinornis santensis*, and (**D**) *Archaeopteryx lithographica*.

P. C. Sereno, Department of Organismal Biology and Anatomy, and Committee on Evolutionary Biology, University of Chicago, Chicago, IL 60637.
Rao C., Beijing Natural History Museum, Beijing, People's Republic of China.

*To whom correspondence should be addressed.

(*14*), which provides lift and enhances maneuverability and braking during landing.

The pectoral girdle and forelimb show many features related to advanced wing design and the avian flight stroke and a reduction of the grasping capability manifest in *Archaeopteryx* and theropod outgroups. The glenoid socket that articulates with the humeral head faces laterally, rather than posteroventrally, permitting excursion of the humerus above the vertebral column during the flight stroke. The second, or middle, digit of the manus and the ulna support the primary and secondary flight feathers, respectively, and each is correspondingly more robust than adjacent long bones; in *Sinornis* the second digit and ulna are twice the diameter of the first digit and radius, respectively, rather than subequal as in *Archaeopteryx* and theropods.

The wrist joint in living birds is modified to permit the wing to fold tightly, reducing drag during the recovery phase of the flight stroke (small birds) (*15*) and protecting the wing during rest in a compact posture along the side of the trunk. The wing most often assumes this retracted (flexed) position upon death, apparently due to passive contraction of forelimb ligaments (*14*). *Sinornis* exhibits both positional and osteological evidence, which suggests that such an advanced wing-folding mechanism was present. As preserved, the right manus and forearm in the holotype skeleton are flexed at an angle of about 70° (Fig. 2B). In *Archaeopteryx* or other maniraptoran theropods, in contrast, the manus and forearm have never been preserved in articulation at an angle of flexion less than 90° (Fig. 3, A and B). Also in *Sinornis*, the large heart-shaped ulnare (Fig. 3, C and E) resembles the large V-shaped ulnare in *Ichthyornis* (*5*) and living birds, with the slot accommodating the lateral margin of the manus during hyperflexion. In *Archaeopteryx*, in contrast, the small ovoid ulnare is positioned distally, rather than ventrally, to the ulna (Fig. 3B) (*12*).

In *Sinornis* and all later volant birds, the manus is shorter than either the forearm or humerus, and digit I of the manus is reduced relative to digit II, which supports the primary feathers (Fig. 3, C and D). The manus in *Archaeopteryx* and maniraptoran outgroups, in contrast, exceeds the length of the forearm and humerus and maintains a primitive grasping function, with digit I subequal to digit II in diameter (Fig. 3, A and B).

The pes in *Sinornis* has an opposable (incumbent) hallux for perching. Metatarsal 1 articulates at the distal end of metatarsal 2, and the phalanges of digit I are directed posteriorly in opposition to digits II through

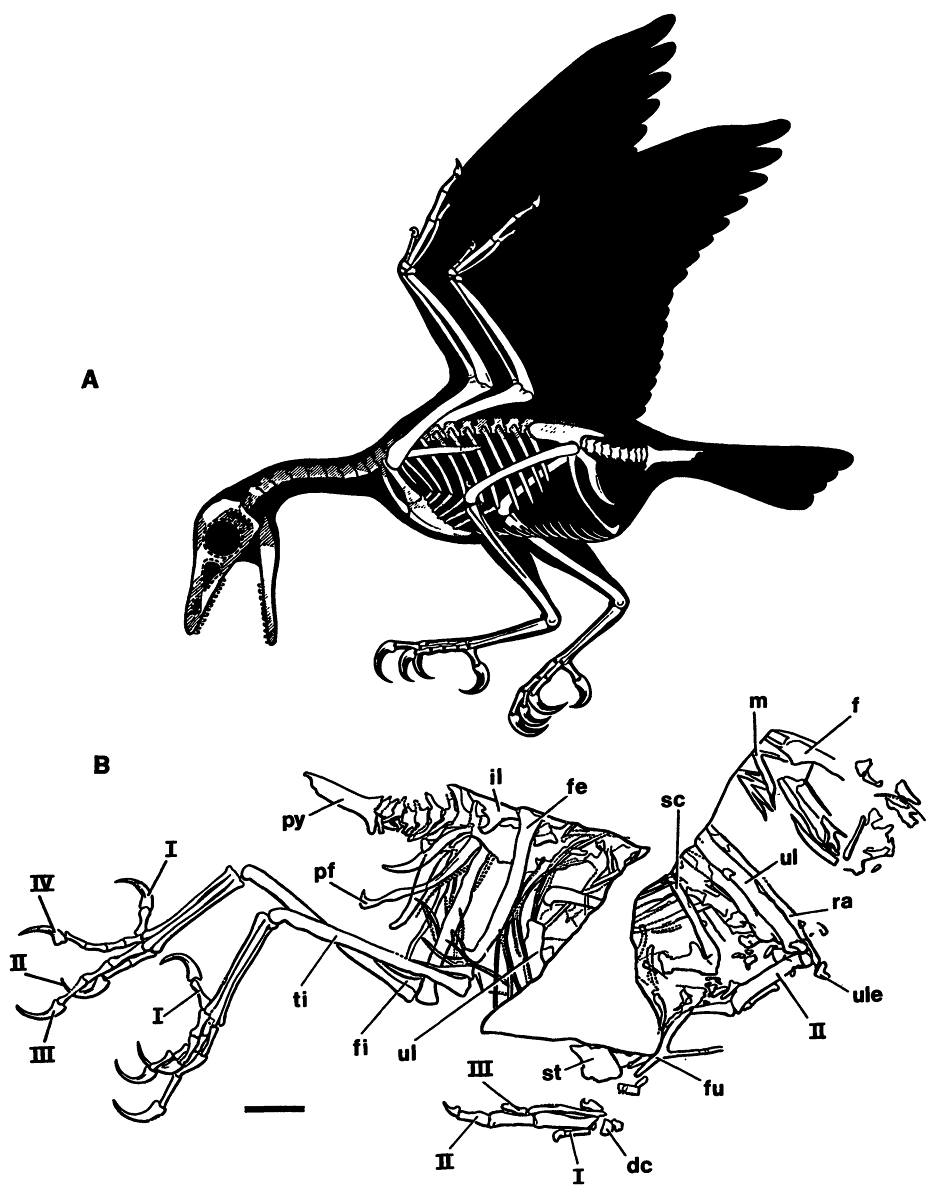


Fig. 2. *Sinornis santensis*, from the Lower Cretaceous of Liaoning Province, China. (**A**) Reconstruction (crosshatching indicates missing parts); (**B**) holotype skeleton as originally preserved on part slab (figure combines information from part and counterpart). I through IV, first through fourth digits; dc, distal carpal; f, frontal; fe, femur; fi, fibula; fu, furcula; il, ilium; m, maxilla; pf, pubic foot; py, pygostyle; sc, scapula; st, sternum; ti, tibia; ul, ulna; ule, ulnare. Scale bar, 1 cm.

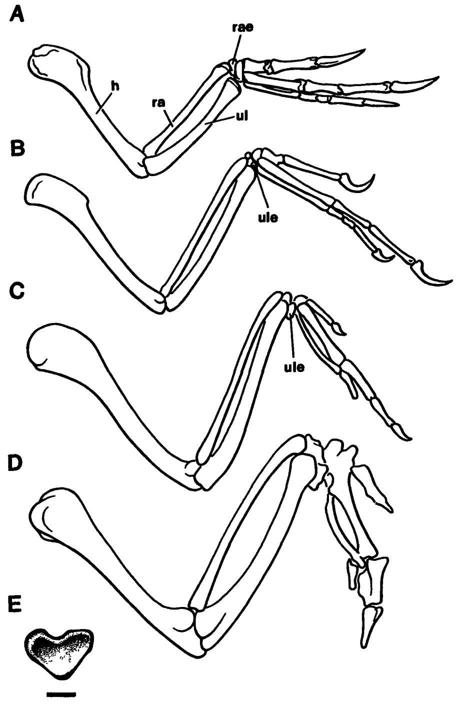
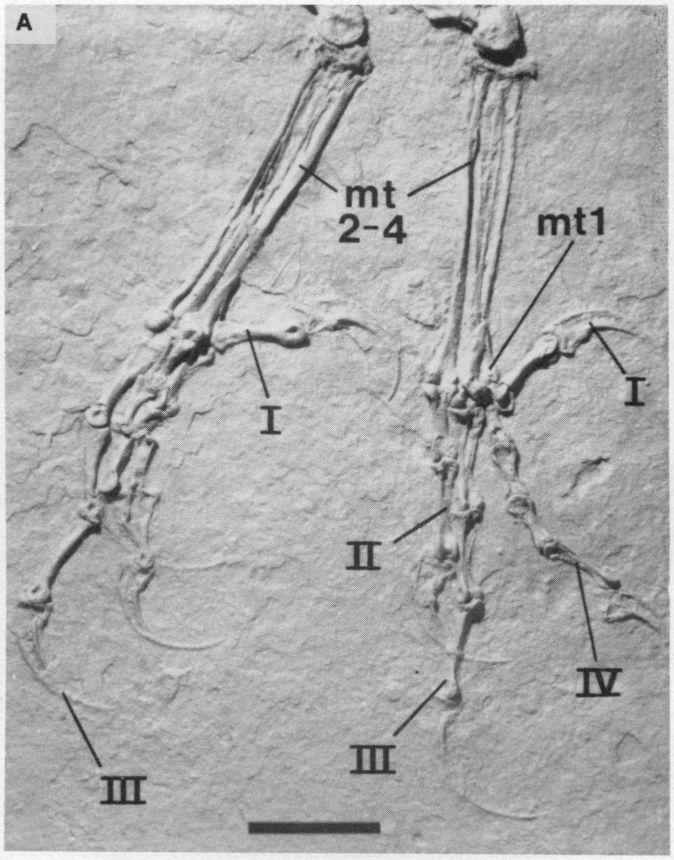


Fig. 3. Forelimb in deinonychosaurian theropods and birds showing maximum flexion of the wrist joint. (**A**) *Deinonychus* (based on articulated casts of YPM 5206, 5208, 5220, and AMNH 3015); (**B**) *Archaeopteryx* [based on the Eichstätt specimen (*12*)]; (**C**) *Sinornis santensis* (based on BNHM BPV538a); (**D**) *Gallus gallus* [from (*14*)]; (**E**) right ulnare (from epoxy cast of natural mold) with 1-mm scale bar; AMNH, American Museum of Natural History; BNHM, Beijing Natural History Museum; h, humerus; ra, radius; rae, radiale; ul, ulna; ule, ulnare; YPM, Yale Peabody Museum.



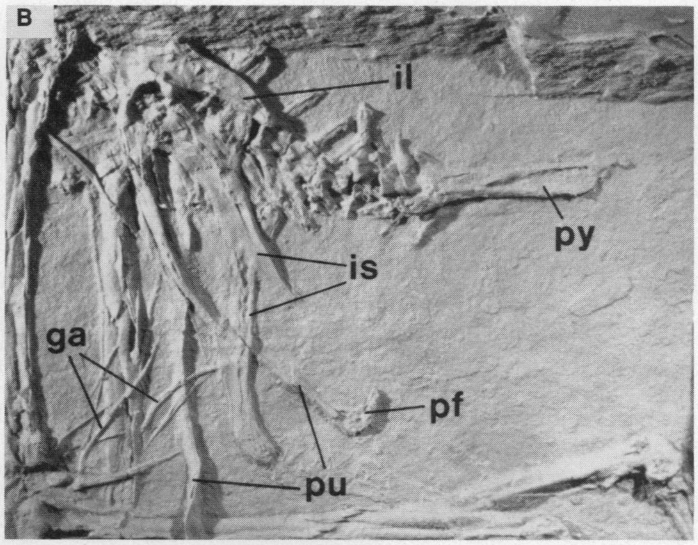


Fig. 4. *Sinornis santensis* postcranium (epoxy cast from natural mold). (**A**) Pedes showing unfused metatarsals (mt), retroverted digit I (I), and highly recurved unguals. Scale bar, 5 mm. (**B**) Pelvis and tail showing the erect ilium (il), blade-shaped ischium (is), pubis (pu) with pubic foot (pf), large pygostyle (py), and gastralia (ga).

IV. The slender, recurved form of the pedal unguals also supports perching and climbing as the primary functional roles of the pedes. The hallux in *Archaeopteryx* (*12*) and *Ichthyornis*, in contrast, is elevated as in extant birds in terrestrial or shore environments. The fifth digit of the pes, which is retained as a reduced metatarsal in *Archaeopteryx*, is absent in *Sinornis* and later birds.

The evolutionary implications of the ancient Chinese avian include the following.

1) *Basal position within Aves*. The archaic features of the skull and postcranial skeleton in *Sinornis* (short snout, teeth, flexible clawed manus, archaic pelvis with footed pubis, gastralia, and limited skeletal coossification) strongly suggest that *Sinornis* occupies a basal position within Aves, as the sister taxon to all other ornithurines (Fig. 5).

2) *Advanced flight function*. Most postcranial modifications in *Sinornis*, compared to the condition in *Archaeopteryx*, are highly significant with regard to flight function. The short trunk and tail shift the center of mass toward the pectoral girdle, transforming a locomotor system based on hind limb thrust (caudofemoralis) during terrestrial locomotion to forelimb lift during flight. The coracoid buttress to the sternum resists compressive forces generated by the principal flight muscles (pectoralis, supracoracoideus). The laterally facing glenoid enhances dorsal excursion of the humerus during the flight stroke. The skeletal supports for the primary and secondary feathers (manual digit II, ulna) are strengthened, and the manus is shortened to increase wing-tip control. The wrist joint is modified for hyperflexion of the manus against the forearm during the recovery phase of the flight stroke and for folding the wing against the trunk during rest. And the distal caudals are fused into a pygostyle for rigid support of rectrices that in living birds provide lift, enhance aerial maneuverability, and function as a brake during landing.

3) *Perching capability*. The large, opposable (incumbent) hallux, the slender, recurved unguals, and the relatively short proportions of the distal limb segments indicate that *Sinornis* could perch and climb (*14*) and probably occupied a predominantly arboreal habitat.

4) *Sustained flight and endothermic physiology*. The simultaneous appearance of advanced flight function and perching capability in *Sinornis*, with concomitant reduction of ancestral cursorial adaptations in the hind limb and tail and grasping function in the manus, suggests that early ornithurines had shifted to an arboreal habitat no more than 15 million years after *Archaeopteryx*. The structure of the flight apparatus suggests that *Sinornis* was capable of sustained flight similar to that in most living birds, powered by bulky aerobic flight muscles and an endothermic physiology. *Archaeopteryx* and maniraptoran theropods, in contrast, retain a primitive theropod pectoral girdle and appear incapable of raising the humerus above the vertebral column or flexing the manus and forearm at an angle less than 90°. Thus, we maintain that *Archaeopteryx* could not fold its wing in a fashion similar to that in volant living birds (*16*). Nonetheless, it is evident from the aerodynamic form and arrangement of flight feathers (*2*) that *Archaeopteryx* was capable of flapping flight of some sort. Indeed *Archaeopteryx* may have been a "flying ectotherm" capable of flight over short distances, powered by lightweight anaerobic flight muscles and an ectothermic physiology as suggested recently by Ruben (*17*). In this scenario, *Sinornis* may document

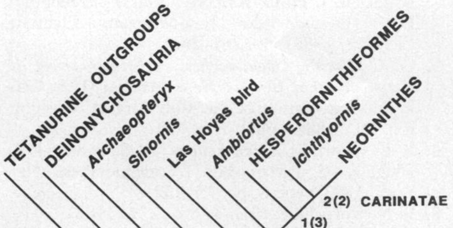


Fig. 5. Cladistic hypothesis of early avian relationships based on a numerical cladistic analysis of 93 osteological characters (*19*) with PAUP (*20*). Numbers at nodes indicate the number of supporting unequivocal synapomorphies (total number of synapomorphies under accelerated-transformation optimization shown in parentheses; consistency index equals 0.91).

the seemingly abrupt appearance in the early Early Cretaceous (Neocomian) of sustained powered flight and endothermic physiology in the first habitually arboreal birds.

5) *Reassessment of early avian phylogeny and ecology*. The advanced flight apparatus and opposable hallux in *Sinornis* and the Spanish bird (*6*) suggest that sustained powered flight and perching capability are primitive for Ornithurae and can no longer be used to unite Ichthyornithiformes and Neornithes to the exclusion of Hesperornithiformes (*18*). These synapomorphies must have been reduced or lost during the evolution of diving habits in Hesperornithiformes. The interrelationships among Late Cretaceous birds are correspondingly less secure, although several additional features maintain a close relationship between Ichthyornithiformes and Neornithes (Fig. 5). Nearly all Mesozoic birds known from reasonably complete remains have been discovered in quiet near-shore marine or marginal lagoon sediments, and this taphonomic bias has colored our view of early avian evolution. The discovery of *Sinornis* in freshwater lake deposits highlights the important, yet largely unknown, role that inland wooded habitats must have played in the early evolution of birds.

REFERENCES AND NOTES

1. J. H. Ostrom, *Smithson. Contrib. Paleobiol.* **27**, 1 (1976); in *The Beginnings of Birds*, M. K. Hecht, J. H. Ostrom, G. Viohl, P. Wellnhofer, Eds. (Freunde des Jura-Museums Eichstätt, Eichstätt, 1985), pp. 161–176; R. A. Thulborn and T. L. Hamley, *Aust. J. Zool.* **30**, 611 (1982); R. A. Thulborn, *Zool. J. Linn. Soc.* **82**, 119 (1984); L. D. Martin, *Doc. Lab. Géol. Lyon* **99**, 9 (1987); J. Cracraft, *Paleobiology* **12**, 383 (1986); in *The Phylogeny and Classification of the Tetrapods*, M. J. Benton, Ed. (Clarendon, Oxford, 1988), vol. 1, pp. 339–361. On the basis of published evidence, we are not convinced that fossil remains recently reported from the Late Triassic of Texas [S. Chatterjee, *Philos. Trans. R. Soc. London B* **332**, 277 (1991)] are avian.
2. A. Feduccia and H. Tordoff, *Science* **203**, 1021 (1979); B. Stephan, in *The Beginnings of Birds*, M. K. Hecht, J. H. Ostrom, G. Viohl, P. Wellnhofer, Eds. (Freunde des Jura-Museums Eichstätt, Eichstätt, 1985), pp. 261–265.
3. O. C. Marsh, *Odontornithes: A Monograph of the Extinct Toothed Birds of North America* (U.S. Geological Exploration of the 40th Parallel, Washington, DC, 1880), publ. 7, p. 201.
4. S. L. Olson, in *Avian Biology*, D. S. Farner, J. R. King, K. C. Parkes, Eds. (Academic Press, New York, 1985), vol. 8, pp. 79–252.
5. E. N. Kurochkin, *Cret. Res.* **6**, 271 (1985).
6. J. L. Sanz, J. F. Bonaparte, A. Lacasa, *Nature* **331**, 433 (1988); J. Cracraft, *ibid.*, p. 389.
7. C. G. Rao and P. C. Sereno, *J. Vert. Paleont.* **10**, 38A (1990).
8. Etymology: *Sino*, China; *ornis*, bird; *santa*, three temples (traditional Chinese name for Chaoyoung county in Liaoning Province where the bird skeletons were found); *ensis*, of a place. The holotype skeleton is cataloged as BPV 538a (part) and BPV 538b (counterpart) in the collections of the Beijing Natural History Museum. *Sinornis santensis* is diagnosed on the saber-shaped ischium and highly recurved pedal unguals.
9. Hao Y. *et al.*, *The Stratigraphy of China: The Cretaceous in China* (The Publisher House of Geology, Beijing, 1986); Hong Y., *Entomotaxonomia* **10**, 128 (1988); Chen P., *Acta Palaeont. Sinica* **27**, 681 (1988).
10. Yu J. *et al.*, *Bull. Chinese Acad. Geol. Sci.* **13**, 93 (1986). The associated spore and pollen assemblage was correlated with beds in Siberia that contain the Valanginian zone-ammonite *Polyptychites* [E. Neaverson, *Stratigraphical Palaeontology* (Clarendon, Oxford, 1955); E. Kemper, in *The Boreal Lower Cretaceous*, R. Casey and P. F. Rawson, Eds. (Seel House, Liverpool, 1973), pp. 327–343; V. V. Drushtchitz and T. N. Gorbatschik, in *Aspekte der Kreide Europas*, J. Wiedmann, Ed. (E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 1979)] and with spore-pollen assemblages in Dorset that suggest a Late Berriasian to Valanginian age.
11. A similar ungual was reported in the second digit of *Ambiortus* (*5*) but the manus is poorly preserved.
12. P. Wellnhofer, *Palaeontogr. Abt.* **147**, 169 (1974); *Archaeopteryx* **6**, 1 (1988); D. W. Yalden, in *The Beginnings of Birds*, M. K. Hecht, J. H. Ostrom, G. Viohl, P. Wellnhofer, Eds. (Freunde des Jura-Museums Eichstätt, Eichstätt, 1985), pp. 91–97.
13. Preservation in lake sediments suggests that the holotype skeleton was probably capable of flight, which occurs in most living birds only after they have achieved adult body size [R. E. Ricklefs, *Ibis* **115**, 177 (1973); *Biol. Rev.* **54**, 269 (1979); D. Carrier and L. R. Leon, *J. Zool. London* **222**, 375 (1990)].
14. R. J. Raikow, in *Form and Function in Birds*, A. S. King and J. McLelland, Eds. (Academic Press, London, 1985), vol. 3, pp. 57–147.
15. F. A. Jenkins, Jr., K. P. Dial, G. E. Goslow, Jr., *Science* **241**, 1495 (1988).
16. We challenge recent reconstructions that show *Archaeopteryx* and *Deinonychus* with the menus hyperflexed. [J. A. Gauthier and K. Padian, in *The Beginnings of Birds*, M. K. Hecht, J. H. Ostrom, G. Viohl, P. Wellnhofer, Eds. (Freunde des Jura-Museums Eichstätt, Eichstätt, 1985), pp. 185–197].
17. J. Ruben, *Evolution* **45**, 1 (1991).
18. 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; J. Cracraft, *Paleobiology* **12**, 383 (1986).
19. P. C. Sereno, in preparation.
20. D. L. Swofford, PAUP 3.0 (Illinois Natural History Survey, Champaign, 1989).
21. Supported by the National Geographic Society (4262-90 to P.C.S.) and the David and Lucile Packard Foundation (to P.C.S.). We thank J. Ostrom for allowing access to fossil materials in his care, W. Simpson for preparation and casting of the skeleton, and C. Abraczinskas for execution of the finished illustrations. We also thank L. Chiappe, J. Cracraft, A. Feduccia, J. Ostrom, and L. Witmer for comments on the manuscript.

10 September 1991; accepted 18 December 1991

Competition, Cooperation, and Mutation: Improving a Synthetic Replicator by Light Irradiation

JONG-IN HONG, QING FENG, VINCENT ROTELLO, JULIUS REBEK, JR.*

Replication and mutation are necessary elements of evolution, and some properties of self-replicating molecules (replicators) can be explored with synthetic structures. Selection and evolution at the molecular level require systems capable of competition and inheritable change. These phenomena have now been observed with synthetic molecules. Two such molecules were prepared having sufficient structural similarity that they catalyzed each other's formation as well as their own. One of the replicators bears a photochemically active function that is cleaved on irradiation. The resulting species is more effective at replication than the original and rapidly takes over the system's resources.

SELF-REPLICATING MOLECULES CAN be synthesized by covalent linkage of two complementary subunits to give a self-complementary structure (*1*). Complementarity in this context refers to sizes, shapes, and the weak intermolecular forces involved in molecular recognition between the two subunits. Behavior such as autocatalysis and sigmoidal product growth can be expressed by these synthetic replicators as well as by nucleic acid derivatives (*2–5*). For the system to evolve, replicators are expected to make "mistakes," or respond to environmental stresses that favor new and more (or less) competitive species (*6*). Accordingly, we have synthesized structures capable of cooperation and mutation and report here their properties.

Coupling of the imide ester **1** (Eq. 1) with amines bearing adenine nuclei **2** in $CHCl_3$ yields the respective amides **3** (*7*). The self-complementarity of these products leads to their extensive dimerization through hydrogen bonding to **4** and is the key to their replicative behavior (*1*).

All three products are replicators: They catalyze their own formation. Specifically, adding 20% of a product to its respective reaction mixture enhances the initial coupling rate by 60% for **3a** and by ~30% for **3b** and **3c** (Figs. 1 and 2). The autocatalysis results from the template effects that gather the two reacting components on the product surface as suggested in Eq. 2. The unsubstituted **3a** can replicate both through Hoogsteen base pairing as shown in **5** and through Watson-Crick pairing as shown in **6**. The urethane-protected **3b** and **3c** are disadvantaged in this respect; the nitrogen substituent hinders base pairing in the Wat-

---

Department of Chemistry, Massachusetts Institute of Technology, Cambridge, MA 02139.

*To whom correspondence should be addressed.