

However, it remains unclear how to scale up these novel devices because of the lack of strategies in scaling up nanotube growth and large-scale nanotube assembly and patterning (1, 30). Using the synthesized self-oriented nanotube arrays without further sample processing, we have studied their properties as electron field emission arrays. About 15 samples have been tested, and they all exhibit low operating voltages and high current stability (Fig. 4). Their performances are comparable to the best field emission samples previously constructed by processing arc-discharge multi-walled or single-walled nanotubes (6, 8–11). Notably, our approach to these useful devices is via direct chemical synthesis of massive arrays of oriented nanotubes on macroscopic substrates.

We have synthesized regular arrays of oriented nanotubes with high uniformity on substrates with typical size ~ 2 cm by 2 cm. Growth on large wafers is currently limited by the size of the CVD chamber. Our synthetic approach involves porous silicon or plain silicon substrates, metal evaporation and annealing for catalyst formation, and CVD, all of which are well within the capabilities of the current silicon technology for fully automated synthesis and production of practical nanotube devices.

References and Notes

- R. Service, *Science* **281**, 940 (1998).
- H. Dai et al., *Nature* **384**, 147 (1996).
- S. Wong et al., *J. Am. Chem. Soc.* **120**, 603 (1998).
- S. Wong et al., *Nature* **394**, 52 (1998).
- H. Dai et al., *Appl. Phys. Lett.* **73**, 1508 (1998).
- W. A. de Heer et al., *Science* **270**, 1179 (1995).
- P. G. Collins and A. Zettl, *Appl. Phys. Lett.* **69**, 1969 (1996).
- Q. Wang et al., *ibid.* **72**, 2912 (1998).
- Q. H. Wang et al., *ibid.* **70**, 3308 (1997).
- J.-M. Bonard et al., *ibid.* **73**, 918 (1998).
- Y. Saito et al., *Ultramicroscopy* **73**, 1 (1998).
- S. Tans et al., *Nature* **393**, 49 (1998).
- W. Li et al., *Science* **274**, 1701 (1996).
- Z. Pan et al., *Nature* **394**, 631 (1998).
- M. Terrones et al., *ibid.* **388**, 52 (1997).
- M. Terrones et al., *Chem. Phys. Lett.* **285**, 299 (1998).
- Z. F. Ren et al., *Science* **282**, 1105 (1998).
- L. T. Canham, *Appl. Phys. Lett.* **57**, 1046 (1990).
- R. T. Collins et al., *Phys. Today* **50**, 24 (1997).
- J.-C. Vial and J. Derrien, Eds., *Porous Silicon Science and Technology: Winter School, Les Houches, 1994* (Springer-Verlag, Berlin, 1994).
- R. L. Smith and S. D. Collins, *J. Appl. Phys.* **71**, R1 (1992).
- G. Che et al., *Nature* **393**, 346 (1998).
- T. Kyotani et al., *Chem. Mater.* **8**, 2109 (1996).
- S. Amelinckx et al., *Science* **265**, 635 (1994).
- R. T. K. Baker, *Carbon* **27**, 315 (1989).
- G. G. Tibbetts, *J. Cryst. Growth* **66**, 632 (1984).
- J. Kong et al., *Chem. Phys. Lett.* **292**, 567 (1998).
- We have grown regular arrays of oriented nanotube blocks on plain Si(100) substrates (we typically use B-doped p-type wafers, resistivity 5 to 10 ohm-cm). The overall structures of the nanotube blocks are similar to those grown on porous silicon. However, in contrast to porous silicon, we often find many nanotube towers with aspect ratio ≥ 5 falling onto the surface. This indicates weaker interactions at the interfaces between the nanotubes and the flat silicon surface. Also, the nanotubes appear to be less well aligned on plain silicon substrates than on the porous silicon. TEM studies show that the nanotubes synthesized on plain silicon sub-

strates have larger diameters and broader diameter distributions than those on porous silicon.

- The growth rate seems to be linear initially and tends to level off at longer time reactions (S. Fan, M. Chapline, N. Franklin, H. Dai, unpublished data).
- D. Normile, *Science* **281**, 632 (1998).
- S.F. is on leave from the Department of Physics,

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Pulmonary Function and Metabolic Physiology of Theropod Dinosaurs

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Ultraviolet light analysis of a fossil of the theropod dinosaur *Scipionyx samniticus* revealed that the liver subdivided the visceral cavity into distinct anterior pleuropericardial and posterior abdominal regions. In addition, *Scipionyx* apparently had diaphragmatic musculature and a dorsally attached posterior colon. These features provide evidence that diaphragm-assisted lung ventilation was present in theropods and that these dinosaurs may have used a pattern of exercise physiology unlike that in any group of living tetrapods.

Lung structure and ventilation in theropod dinosaurs is assumed to have resembled the specialized flow-through, air sac pulmonary system of extant birds, the closest living relatives of the theropods (1). However, some fossil soft tissue evidence, as well as osteological similarities between crocodylians and theropods, suggests that these dinosaurs may have had relatively unmodified septate lungs that were ventilated with the assistance of an active, hepatic piston–diaphragm mechanism (2). Those conclusions are based, in part, on the distinct, vertically oriented, thoracic-abdominal separation of the visceral cavity in the theropod *Sinosauropteryx* (Coelurosauria: Compsognathidae) (Fig. 1, bottom). Additionally, the leading edge of the abdominal cavity in this dinosaur appears to have been defined by a remarkably crocodylian-like, anterior surface of the liver. These attributes, as well as the ubiquitous occurrence among theropods of a triadate pelvis similar to that of crocodylians, well-developed gastralia, and specialized rib morphology (3), suggest that these dinosaurs had a crocodylian-like septate lung that was ventilated, in part, with a hepatic piston diaphragm. Such a diaphragm was

likely to have been powered by diaphragmatic muscles that extended between the pubes, gastralia, and liver (2).

A recently described new theropod from Italy, *Scipionyx samniticus* (Coelurosauria: Maniraptoriformes), contains nearly complete preservation of the articulated skeleton (4). The specimen also has remnants of a variety of soft tissues, including portions of the intestines, liver, trachea, and skeletal muscles (Fig. 1, top). Here we describe these soft tissues and discuss their implications for pulmonary structure and function in *Scipionyx*. We also discuss their significance for earlier conclusions about theropod lung morphology and function.

Portions of the large intestine and trachea of *Scipionyx* are visible and appear to have been preserved in situ (Fig. 1) (4, 5). Notably, the posterior colon, or colorectal intestine, is situated far dorsally, at about the same level as the vertebrae in the lumbar-sacral region. This condition is comparable to the position of the colon in living taxa such as crocodylians and mammals (Fig. 2A) (6). In contrast, the colon (or rectum) of birds is invariably suspended by the dorsal mesentery (mesocolon) so that it is situated in the mid-abdominal cavity, some distance from the roof of the cavity (Fig. 2B) (7). This mid-abdominal suspension of avian large (and small) intestines provides a distinct segregation of the colon from the dorsally and medially attached abdominal air sacs (which extend caudally from the dorsally attached parabronchi). Therefore, it is unlikely that avian-style, abdominal air sacs were present in *Scipionyx*. Abdominal air sacs are of fundamental importance to the function of both neo- and paleopulmo por-

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tions of the lung in extant birds (8). Their likely absence in *Scipionyx* is an indication that an avian style, flow-through, air sac lung was not present in this theropod.

A section of the trachea is preserved in the posterior cervical region, immediately anterior to the scapulocoracoid complex (4). Like the trachea of crocodilians, *Scipionyx*'s trachea in this region is situated well ventral to the vertebral column. In contrast, except in specialized, long-necked birds, the avian posterior cervical trachea is usually positioned dorsally and adjacent to the vertebral column, thereby facilitating entry of the trachea into the dorsally attached parabronchi (9).

In visible light, *Scipionyx*'s liver appears as a small hematic halo restricted to the ventral margin of the visceral cavity (4, 5). However, the liver is more accurately visualized under ultraviolet illumination, where it fluoresces as a suboval, indigo-colored mass that extends from the vertebral column to the ventral body wall (Fig. 1) (10). As in crocodilians, *Scipionyx*'s liver is situated ahead of the large intestine and fills the anteriormost portion of the abdominal cavity (2). Furthermore, as in crocodilians and the theropod *Sinosauropteryx* (Fig. 1), the anterior border of the liver in *Scipionyx* is vertically oriented and completely subdivides the visceral cavity into anterior pleuropericardial and posterior abdominal regions (2). In both *Scipionyx* and *Sinosauropteryx*, the pleuropericardial cavity appears largely empty because delicate lung tissues were not fossilized.

Hepatic piston, diaphragm-assisted breathing in crocodilians is powered by the diaphrag-

matic muscles that originate on the gastralia and distinctly shaped pubes and insert on the lateral surfaces of the liver (2). As in other theropods, the triradiate pelvis of *Scipionyx* is remarkably like that of modern and, especially, basal crocodilians (such as protosuchids): in particular, the rodlike rami of the pubes are elongate with a marked distal expansion, or "boot" (Fig. 3) (11). In living crocodilians, these osteological features are particularly well suited to accommodate diaphragmatic muscle function (2). Specifically, the stout, rodlike pubic rami most likely provide enhanced stability required to withstand contractile force of the extensive diaphragmatic muscles; the expanded pelvic boot in crocodilians is necessary to allow sufficient area for attachment of the ventral portion of the diaphragmatic muscles.

Significantly, a small group of longitudinally oriented muscle fibers that extend anteriorly from the right pubis in *Scipionyx* appear to be remnants of the diaphragmatic musculature (Figs. 1 and 3) (12). The position and orientation of these fibers resemble some of the posteriormost lateral diaphragmatic muscle fibers in crocodilians (2). The longitudinally oriented, deep external oblique muscle is also found in this region in extant reptiles (13). However, it is unlikely that these fibers in *Scipionyx* were components of this muscle. Tetrapods with parasagittal limb posture, such as theropods, would be unlikely to have had longitudinally oriented flank musculature; such musculature is associated with the production of lateral bending of the trunk during locomotion in animals, such as lizards, that have a sprawling posture (13).

Together, these features are consistent with *Scipionyx* having used hepatic piston, diaphragm-assisted breathing (similar to that which occurs in extant crocodilians) and with hypothesized breathing mechanisms for *Sinosauropteryx* (2). These attributes are inconsistent with *Scipionyx* having had an avian-style, lung air sac system. Moreover, data indicative of diaphragm breathing in such disparate forms as *Sinosauropteryx* and *Scipionyx* reinforce the hypothesis that diaphragm-assisted lung ventilation was widespread in

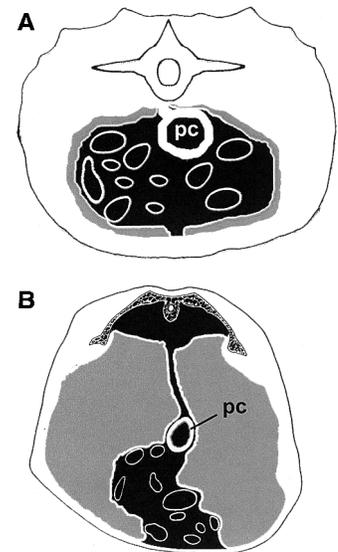


Fig. 2. Schematic representation of the relation of the posterior colon (pc) to the roof of the abdominal cavity in (A) crocodilians and (B) birds. Areas in gray represent the coelomic cavity. Unlike crocodilians and the theropod *Scipionyx*, the posterior colon of birds is situated some distance from the roof of the visceral cavity. In birds, abdominal air sacs occupy the dorsal abdominal cavity [(B) modified from (7)].

Fig. 1. Similar body cavity partitioning in two theropods, *Scipionyx* (top) and *Sinosauropteryx* (bottom; image digitally reversed for purposes of comparison). Anterior is to the right. Arrows indicate the probable anterior border of the liver, which formed a distinct, vertical subdivision of the pleuropericardial and abdominal cavities. Note also the dorsal position of the posterior colon in *Scipionyx*. The image of *Scipionyx* was recorded under ultraviolet illumination. Abbreviations: c, colon; pc, posterior colon; *, diaphragmatic muscles; **, pectoral girdle musculature. *Scipionyx* specimen courtesy of Soprintendenza Archeologica, Salerno, Italy.

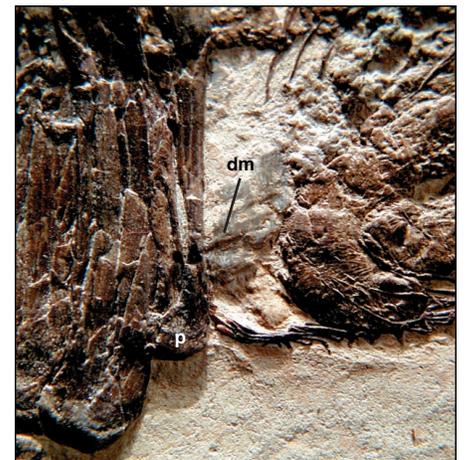
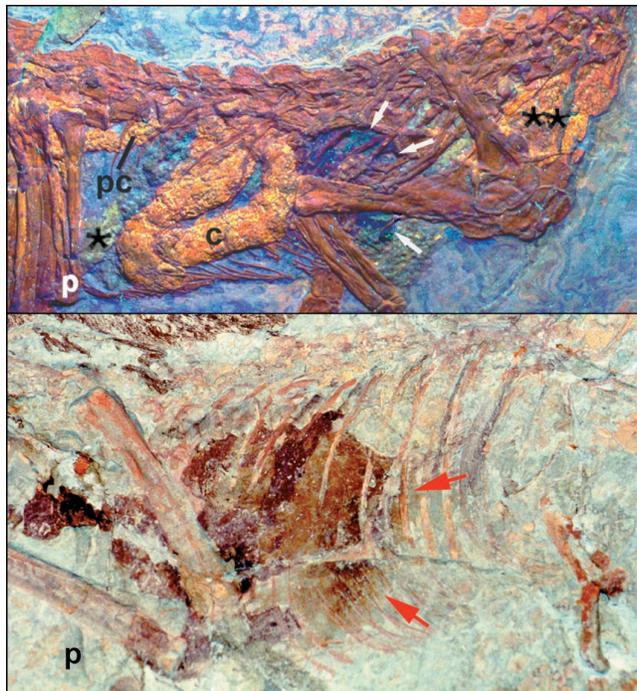


Fig. 3. Probable remnants of the diaphragmatic muscles in *Scipionyx*. Portions of pectoralis and caudofemoralis muscles are also preserved in the specimen. Abbreviations: dm, diaphragmatic muscle; p, pubis. Specimen courtesy of Soprintendenza Archeologica, Salerno, Italy.

theropod dinosaurs.

The absence of respiratory turbinates in theropod dinosaurs indicates that they were likely to have maintained ectotherm-like resting, or routine, lung ventilation and metabolic rates (14). As in extant reptiles (for example, *Varanus*), costal breathing seems adequate to have supported active rates of oxygen consumption in such animals. Consequently, on the basis of the physiology of extant, fully terrestrial ectotherms, the necessity for a specialized diaphragm to supplement costal lung ventilation in theropods would seem anomalous. However, recent analysis suggests that expansion of lung ventilatory capacity might have allowed the relatively unmodified separate lungs of dinosaurs to have achieved active rates of O₂-CO₂ exchange that might have approached, or even overlapped, those of a few extant mammals (15). Perhaps the presence of diaphragm-assisted lung ventilation in theropods indicates that, although these dinosaurs maintained ectotherm-like routine metabolic rates, they were, nevertheless, capable of sustaining active oxygen consumption rates and activity levels well beyond those of even the most active living reptiles. Such a pattern of metabolic physiology is unknown in extant tetrapods.

This pattern of metabolic physiology in theropods might seem inconsistent with the presence of a hepatic-piston diaphragm in extant crocodylians, none of which appears to have particularly enhanced capacity for oxygen consumption during exercise (16). However, relatively low aerobic capacity in recent crocodylians, all of which are aquatic, might not represent the ancestral condition. Early (Triassic) crocodylomorphs (for example, *Protosuchus* and *Terrestriusuchus*) might have had enhanced aerobic capacities because they appear to have been fully terrestrial and cursorial with habitually upright limb posture (17).

References and Notes

1. R. E. Reid, in *The Complete Dinosaur*, J. O. Farlow and M. K. Brett-Surman, Eds. (Indiana Univ. Press, Bloomington, 1997), pp. 449–473.
2. J. A. Ruben, T. D. Jones, N. R. Geist, W. J. Hillenius, *Science* **278**, 1267 (1997).
3. R. Hengst, *ibid.* **281**, 47 (1998).
4. C. Dal Sasso and M. Signore, *Nature* **392**, 383 (1998).
5. _____, in *Third European Workshop of Vertebrate Paleontology-Maastricht*, J. W. M. Jagt, P. H. Lambers, E. W. A. Mulder, A. S. Schulp, Eds. (Naturhistorisches Museum, Maastricht, The Netherlands 1998), p. 23.
6. R. B. Chiasson, personal communication. Figure 2A was drawn from original dissections of three specimens of *Alligator*.
7. H.-R. Duncker, in *Form and Function in Birds*, A. S. King and J. McLelland, Eds. (Academic Press, New York, 1989), vol. 1, pp. 39–67.
8. _____, *Adv. Anat. Embryol. Cell Biol.* **45**, 1 (1971); P. Scheid and J. Piiper, in (7), vol. 4, pp. 369–388.
9. J. McLelland, in (7), vol. 4, pp. 69–100.
10. Under UV illumination [provided with an 80-watt, mercury vapor incandescent bulb (350 to 400 nm)], the dark blue-indigo fluorescence of the liver in *Scipionyx* is distinct from that of any other structure in the specimen or the surrounding matrix. Available

evidence indicates that biliverdin is a predominant liver bile pigment present in nonmammalian tetrapods [T. K. With, *Bile Pigments* (Academic Press, New York, 1968)]. Fluorescence of biliverdin includes a primary light emission peak at about 470 nm, which corresponds to the blue region of the spectrum of visible light [P.-S. Song *et al.*, *J. Am. Chem. Soc.* **95**, 7892 (1973)]. Thus, coloration of *Scipionyx's* liver under ultraviolet illumination is possibly consistent with the presence of liver bile pigment residues in this region of the specimen (P. E. Hare, personal communication).

11. A. S. Romer, *Osteology of the Reptiles* (Univ. of Chicago Press, Chicago, IL, 1956).
12. Under ultraviolet illumination, the texture and fluorescence of these diaphragmatic muscle fibers, although apparently not well fossilized, are distinct from the surrounding matrix and are generally similar to that of previously described portions of the caudofemoralis and pectoral girdle muscles in *Scipionyx*. Identification of this element as a remnant of the diaphragm musculature is based primarily on its lon-

gitudinal, fanlike, fibrous structure and its location in the specimen. Both of these features conform closely to corresponding portions of the diaphragmatic muscle in living crocodylians.

13. D. R. Carrier, personal communication; *J. Exp. Biol.* **152**, 453 (1990).
14. J. A. Ruben *et al.*, *Science* **273**, 1204 (1996).
15. J. W. Hicks and C. G. Farmer, *ibid.* **281**, 45 (1998); J. A. Ruben *et al.*, *ibid.*, p. 47.
16. A. F. Bennett, R. S. Seymour, G. J. W. Webb, *J. Exp. Biol.* **118**, 161 (1985).
17. D. R. Carrier, *Paleobiology* **13**, 326 (1987); E. H. Colbert and C. C. Mook, *Bull. Am. Mus. Nat. Hist.* **97**, 143 (1951).
18. We thank G. Tocco and C. Sloan for assistance in obtaining access to specimens used in this study. Supported by The College of Charleston, Charleston, SC, and an NSF grant IBN-9420290 to W.J.H. and J.A.R.

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An ~15,000-Year Record of El Niño–Driven Alluviation in Southwestern Ecuador

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Debris flows have deposited inorganic laminae in an alpine lake that is 75 kilometers east of the Pacific Ocean, in Ecuador. These storm-induced events were dated by radiocarbon, and the age of laminae that are less than 200 years old matches the historic record of El Niño events. From about 15,000 to about 7000 calendar years before the present, the periodicity of clastic deposition is greater than or equal to 15 years; thereafter, there is a progressive increase in frequency to periodicities of 2 to 8.5 years. This is the modern El Niño periodicity, which was established about 5000 calendar years before the present. This may reflect the onset of a steeper zonal sea surface temperature gradient, which was driven by enhanced trade winds.

The dramatic effects of the 1997–98 El Niño event have highlighted several shortcomings in our understanding of the El Niño–Southern Oscillation (ENSO) phenomenon (1). These shortcomings include the age of onset of modern ENSO variability, long-term (>10³ years) changes in the frequency of past extreme El Niños and their relation with varying oceanic and atmospheric states, and the frequency and magnitude of the ENSO in Earth's greenhouse future. High-resolution records of prehistoric El Niños are needed to address these questions.

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Proxy records of prehistoric El Niños have been obtained from a variety of archives, including corals, ice cores, tree rings, flood deposits, beach ridges, archeological middens, and soils (2, 3). However, high-resolution coral and ice core records (4) have been limited to the past two millennia, and longer proxy records of El Niños from the tropical Pacific region are inherently discontinuous (3, 5). Here, we present a high-resolution record of storm-derived clastic sedimentation that spans the past 15,000 years and appears to record El Niño events.

Sea surface temperatures (SSTs) near Guayaquil, Ecuador, are some of the first to warm in the region of upwelling along the coasts of Perú and Ecuador during the onset of an El Niño event (1), and typically, rainfall in this region greatly increases over background levels during the onset of strong to very strong (hereafter, severe) (6) El Niños. The mature phase of El Niño, in which the zonal SST gradient is at a minimum, occurs just as the normal austral summer rainy season in western Ecuador begins. During stron-