controls and from the treated plants are shaped like the pieces of a jigsaw puzzle. It seems that both submergence and gibberellic acid cause these cells to become much more attenuated, and thus the developing leaves become transformed into the long, narrow water forms. The emphasis on cell expansion as the principal control mechanism is further supported by preliminary counts of ordinary epidermal cells: the number of these cells in the two leaf forms in the control conditions differed by only 25 percent or less.

Aquatic angiosperms respond to an environmental change in water status quite differently from other aquatic plants. Almost all estuarine algae studied to date are able to maintain constant turgor pressure in the presence of a wide range of salinities. This regulation is accomplished by exchanging certain ions with the surrounding water or by alternating the level of photosynthate in the cytoplasm (*5*). These mechanisms allow the algae to avoid plasmolysis even when the level of salinity in the estuary approaches that of pure seawater. In contrast, it is the osmotic potential of the angiosperm *C. heterophylla* that exhibits little variation with marked fluctuations in the water status of its environment. Consequently, when a declining water level places the shoot apex of a submerged plant above the water's surface, the newly emergent apex must experience a substantial reduction in cellular turgor, and the pattern of leaf production changes to the land form. Other features associated with this morphological switch are increases in stomatal density and vein number, which help to adapt the leaf for photosynthesis in the aerial environment.

Cell expansion is the essential growth process whereby plant structures increase in size. Internal water relations exert profound effects on the cellular growth rates of such structures as roots, stems, leaves, and coleoptiles (*6*). Furthermore, theoretical studies have shown that the water potentials of cells elongating as a coordinated unit in multicellular structures necessarily decrease with distance from the source of the water supply (*7*). From the present experiments, it appears that the relative amount of cell expansion also determines the overall shape of mature organs, or least in the instance of the leaves of aquatic angiosperms.

In conclusion, the research described here suggests that the relative magnitude of cellular turgor pressure determines leaf form in aquatic angiosperms in their native environment. Moreover, under control and experimental conditions the process of cell expansion affects not only final leaf size but also final leaf shape in aquatic angiosperms. Whether these observations apply to other plants awaits future research.

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A Fossil Noctuid Moth Egg from the Late Cretaceous of Eastern North America

Abstract. *A moth egg assignable to the family Noctuidae (Lepidoptera) is described from 75-million-year-old sediments from Martha's Vineyard, Massachusetts. This sample, which extends the fossil record of this family and modern heteroneuran moths back to the Cretaceous, may provide insight into the coevolution of moths and flowering plants, as well as have implications for the evolution of bats.*

Although the order Lepidoptera is one of the most diverse modern groups, it is underrepresented in the fossil record. The origin and radiation of the Lepidoptera are now thought to have occurred in at least Mesozoic times (*1–3*). Reports of fossil Lepidoptera of Tertiary age now include over 70 moths and 40 butterflies (*4*); the Cretaceous record consists of only a few adults (*3, 5*), larvae (*6*), and wing scales (*7*) of homoneurous Lepidoptera. Reports of the group in the Triassic include *Eoses triassica* (*8*) and material from South Africa (*9*) and Australia (*2*). Some investigators place these early fossils in Mecoptera (*1–3, 10*), and most agree that the Lepidoptera must have been present in the Triassic. Our report of fossil evidence of the vast moth family Noctuidae and of a heteroneurous lepidopteran in the Cretaceous is thus not unexpected. We are not aware of other descriptions of fossil lepidopteran eggs as such, but unidentified fossil "angiosperm seeds" (*11*) may prove to be lepidopteran (or other insect) eggs.

The egg was found in an organic-rich clay lens in lagoonal sediments of the (?)Magothy Formation on Gay Head, Martha's Vineyard. These sediments are dated as earliest Campanian (~ 75 million years old) on the basis of pollen analysis (*12*). The clay contains an array of vegetable remains including conifers (*12, 13*) and a diverse flora of angiosperm flowers, fruits, and seeds (*14*). The angiosperm fossils are less than 3.0 mm in diameter, requiring collection by sieving and examination with a dissecting microscope. The egg was found with plant material in this manner.

The ovoid to broadly ovoid, slightly flattened egg is approximately 500 to 600 μm in diameter and 600 μm high (Fig. 1, a and c). The surface is traversed by about 18 to 20 thick longitudinal ridges, at least one of which bifurcates in the lower hemisphere (extreme left, Fig. 1c). Each longitudinal ridge is connected to its neighbor by 15 to 20, smaller, latitudinal ridges. This surface pattern is stronger than that seen in comparable modern eggs (Fig. 1d). Inspection of the ridges at higher magnification gives no indication of aeropyles—conduits for gas exchange that are present in many modern insect

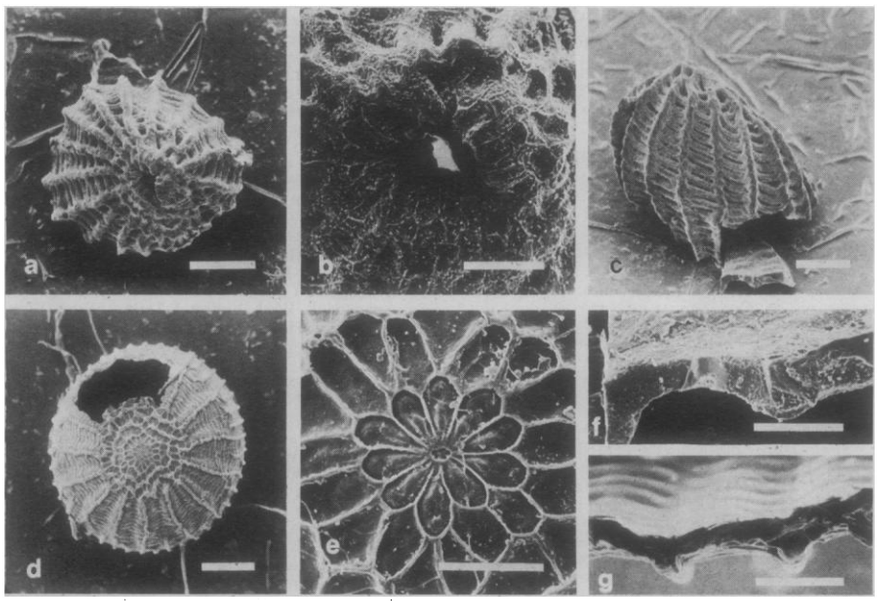

Fig. 1. (a) Fossil noctuid egg. Compare surface sculpture to that in (d) and note apical micropyle at center of egg. Scale bar, 200 μm. (b) Detail of fossil egg micropyle. Although the surface pattern is weakened by fossilization, it is similar to that in (e). Scale bar, 50 μm. (c) Side view of fossil egg. Note coarse surface sculpture and thickness of the wall where broken. Scale bar, 200 μm. (d) Modern egg of *Catocala cara*, with apical micropyle at center and exit hole of larva above. Scale bar, 200 μm. (e) Detail of micropyle of *Catocala cara*. Compare to (b). Scale bar, 50 μm. (f) Cross section of wall of fossil egg, inner side above. Compare thickness to that of (g). Scale bar, 50 μm. (g) Standard electron microscope cross section of wall of *Catocala cara*, inner side above. Scale bar, 50 μm.

eggs. Because both the diameter and size of aeropyles vary considerably even in eggs of closely related insect species (*15*), we cannot be certain of their absence. The egg wall is generally 100 to 150 μm thick (Fig. 1f), which is considerably thicker than most modern lepidopteran eggs (for example, the relatively thick wall of the egg of a modern noctuid, *Catocala cara* Guenee in Fig. 1, d and g). The micropylar region of the fossil (Fig. 1b) is surrounded by a surface pattern of low ridges, which circumscribe 15 to 20 oblong "cells," each 30 to 50 μm long. The cells radiate from the micropyle and gradually merge into the longitudinal ridges. This pattern is similar to that around the micropyles of modern noctuid eggs (Fig. 1e). The micropylar opening of the fossil appears to have been widened in the process of fossilization.

The size, general shape, and surficial ornamentation of the fossil clearly rule out its assignment to any of the 20 nonlepidopteran orders described by Hinton (*15*) as well as to Palearctic Lepidoptera eggs in Doring (*16*), Sarlet (*17*), and Hinton (*15*). Among butterfly eggs examined, the fossil egg only roughly resembles a few nymphalids and, more closely, pyrgine skippers; it is not as elongate as eggs of pierids, nor as ornately sculptured as those of lycaenids. Among moth eggs, there is some similarity to the eggs of cossids, although it is much larger than other modern homoneuran eggs. The fossil egg resembles those of only two heteroneuran families; it has some similarities to those of drepanids and is a close match to those of many noctuids.

Photographs were taken with the scanning electron microscope (SEM) of eggs of several species of the non-noctuid Lepidoptera that we considered most similar to the fossil. Many of these species presently occur at Martha's Vineyard or coastal New England; among them was a cossid (*Prionoxystus macmurtrei*), a drepanid (*Drepana arcuata*), and a pyrgine skipper (*Erynnis horatius*). We also examined SEM photographs of eggs of Holarctic *Catocala* and other noctuids from a broader study of the noctuid egg morphology (*18*). The fossil was distinct from all eggs examined except those of the noctuids, which it resembled closely, particularly in the continuity of the surface pattern between the micropylar region and the lateral walls. All our evidence supports the assignment of the fossil egg to the heteroneurous moth family Noctuidae.

The presence of noctuids in the Cretaceous adds to the evidence (*4*, *19*) for an early- to mid-Mesozoic radiation of the major phyletic lines of the Lepidoptera (*1–3*). Although moth pollination in general is poorly known, the available information suggests that noctuids are important as pollinators of angiosperms (*20*). Certainly many noctuid larvae are specialized to angiosperm host plants to the degree that they are severe economic pests (*21*). Noctuids appear to be coadapted to at least some degree with modern flowering plants. Recent paleobotanical evidence (*22–24*) suggests that angiosperms evolved rapidly in the latest Cretaceous and early Tertiary. Crepet (*23*) has linked this event with the appearance and diversification of modern pollinators in the latest Cretaceous, perhaps aided by the simultaneous or immediately subsequent evolution of modern dispersal agents (*24*). It is thus significant to encounter a late Cretaceous egg of a moth family that has complex relationships with angiosperms in the present day.

The Noctuidae have tympanic organs capable of detecting the ultrasonic echolocation cries of bats, which helps them evade the attacks of these predators (*25*). This complex adaptation, which occurs in several moth families, is found throughout the noctuids. This raises questions about the origin of such an adaptation in that fossil bats are known only as far back as the early Eocene (*26*) and insectivory is considered primitive in the group, and similar flying predators with high-frequency echolocation are not known in the fossil record.

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Primitive Ducts of Renal Dysplasia Induced by Culturing Ureteral Buds Denuded of Condensed Renal Mesenchyme

Abstract. *Primitive ducts, the histological hallmark of human renal dysplasia, were induced in chick embryos by culturing ureteral buds denuded of condensed metanephrogenic mesenchyme.*

Human renal dysplasia, a relatively common malformation, is diagnosed by noting "primitive ducts" in biopsy specimens. The primitive duct is lined by a tall epithelium and is surrounded by a collar of whorled fibromuscular cells (*1*). The duct has been believed to result from injury to the branches of the ureteral bud, but to our knowledge there is no evidence to support this.

In an attempt to clarify the morphogenesis of the primitive duct and thereby improve our understanding of the etiology of renal dysplasia, we studied the development of renal blastemas isolated from chick embryos. We found that (i) isolated renal blastemas grafted onto a chorioallantoic membrane in ovo develop histologically normal renal architecture; (ii) when isolated renal blastemas are cultured in vitro, the ureteral bud branches lose the apposed condensed metanephrogenic mesenchyme; (iii) ureteral buds denuded of condensed metanephrogenic mesenchyme by preliminary tissue culture develop further in ovo as chorioallantoic grafts and form primitive ducts; and (iv) primitive ducts induced in the chick resemble those noted in human renal dysplasia. These findings suggest that the primitive duct of renal dysplasia originates from branches of the ureteral bud that develop without condensed metanephrogenic mesenchyme.

Normal nephrogenesis in the human embryo requires interactions in the renal blastema (*2*), which consists of the ureteral bud and the metanephrogenic mesenchyme. The ureteral bud branches as an arcade and develops into the ureter, pelvis, calyces, and collecting ducts. The metanephrogenic mesenchyme apposes the ampullae of the ureteral bud branches and develops into renal tubules and glomeruli.

Although approximately 10 percent of children are born with potentially significant malformations of the urinary tract (*3*), the morphogenesis of most renal malformations is unknown. Current views are that renal dysplasia arises in utero as the result of abnormal interaction between the ureteral bud and

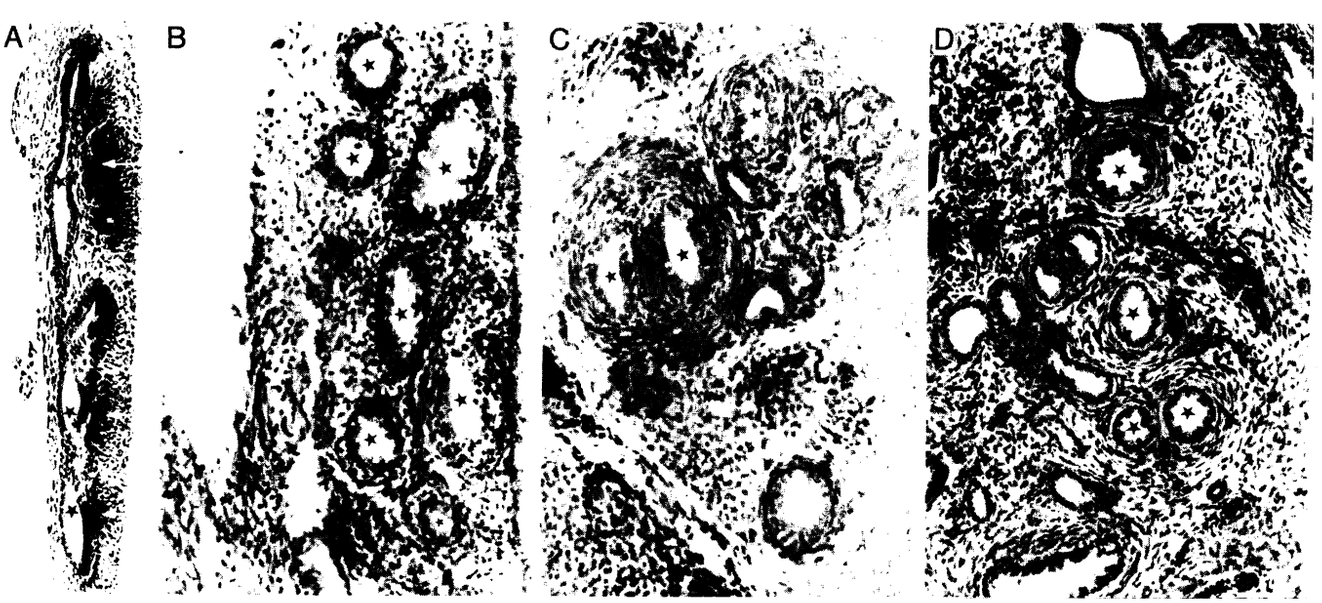

Fig. 1. Induction of primitive ducts. (A) Longitudinal section of renal blastema microdissected from chick embryo after 8 days of incubation. Visible are segmental branches of the ureteral bud (★) and condensed metanephrogenic mesenchyme (arrow) (×160). (B) Renal blastema microdissected from chick embryo after 7 days of incubation and then cultured in vitro for 3 days. Ureteral bud branches (★) are numerous, but the metanephrogenic mesenchyme is no longer condensed or apparent. Renal tubules do not develop in vitro (×160). (C) Renal blastema microdissected from chick embryo after 8 days of incubation, then cultured in vitro for 7 days to provide branched ureteral buds without condensed metanephrogenic mesenchyme, and finally further cultured in ovo as a graft that developed into tissue composed primarily of primitive ducts (★). The ducts are lined by tall epithelium and are surrounded by whorled mesenchymal cells (×160). (D) Nephrectomy specimen in newborn with prune belly syndrome. Primitive ducts (★) typical of renal dysplasia are surrounded by whorled fibromuscular cells and resemble those induced in the chick embryos (×100).