Laonastes and the "Lazarus Effect" in Recent Mammals

Mary R. Dawson,[1*] Laurent Marivaux,[2] Chuan-kui Li,[3] K. Christopher Beard,[1] Grégoire Métais[1]

The living Laotian rodent *Laonastes aenigmamus*, first described in early 2005, has been interpreted as the sole member of the new family Laonastidae on the basis of its distinctive morphology and apparent phylogenetic isolation from other living rodents. Here we show that *Laonastes* is actually a surviving member of the otherwise extinct rodent family Diatomyidae, known from early Oligocene to late Miocene sites in Pakistan, India, Thailand, China, and Japan. *Laonastes* is a particularly striking example of the "Lazarus effect" in Recent mammals, whereby a taxon that was formerly thought to be extinct is rediscovered in the extant biota, in this case after a temporal gap of roughly 11 million years.

In recent years, tropical southeast Asia has been recognized as an important "hot spot" for modern biological diversity (*1*). The latest addition to the mammalian biota of this hot spot is the rodent *Laonastes aenigmamus*, recently described by scientists working on a biodiversity survey in Laos (*2*). Initial investigations of its morphological and molecular affinities established that *Laonastes* is phylogenetically divergent from other living rodents, which led to its classification in the new family Laonastidae. Current knowledge of *Laonastes*, known locally as the kha-nyou, is based on whole specimens that were purchased in local markets and individual bones collected from owl pellets and cave deposits. Although living individuals have yet to be observed by biologists, *Laonastes* seems to be nocturnal in its activity pattern and is thought to inhabit karstic terrain. It has a vaguely squirrel-like appearance, with an elongated head, pelage ranging from black to grizzled, and a long hairy tail. Its jaws and dentition are highly distinctive, having an enlarged hystricomorphous infraorbital foramen, lacking development of the coronoid process on the mandible, and having distinctly bilophodont cheek teeth. The postcranial skeleton, on the other hand, is generalized, suggesting a scampering mode of locomotion.

Although initial phylogenetic results indicated that *Laonastes* pertains to an ancient phylogenetically isolated lineage of rodents, morphological comparisons with fossil rodents have not been undertaken previously. Our familiarity with the fossil record of Asian rodents led us to make extensive comparisons between *Laonastes* and the otherwise extinct Diatomyidae, known from early Oligocene to late Miocene strata in Pakistan, India, Thailand, China, and Japan (*3*–*10*). Three fossil genera—*Fallomus*, *Diatomys*, and *Willmus*—are currently recognized in the Diatomyidae. *Fallomus* is known from isolated teeth and fragments of jaws from the Oligocene and early Miocene of Pakistan, India, and Thailand (*4*, *7*, *8*), whereas the poorly documented *Willmus* is known from two isolated teeth from the late Miocene of Pakistan (*10*). *Diatomys*, on the other hand, is better known and more widely distributed, having Miocene records in Shandong and Jiangsu provinces in eastern China, Kyushu Island in Japan, northern Pakistan, and the Lamphun district of Thailand (*3*, *5*).

Diatomys shantungensis was originally described from the late early Miocene Shanwang Series of Shandong Province, China, based on two relatively complete (but laterally compressed) partial skeletons (*3*). The well-preserved dentitions of these specimens show that the cheek teeth in each jaw quadrant include one premolar and three molars displaying a simple transversely bilophodont occlusal pattern. Details of cranial and mandibular anatomy were difficult to interpret because of the lateral compression of the fossils. However, *Diatomys* was originally thought to have an unenlarged infraorbital foramen (the sciuromorphous condition) and a sciurognathous lower jaw. Its postcranial skeleton lacks any obvious morphological adaptations for either leaping or burrowing.

In June 2005, a new and less compressed specimen of *D. shantungensis* was discovered from the type locality in Shandong Province. The new specimen, IVPP V12692, complete with whiskers and traces of pelage (Fig. 1, A to C), clarifies aspects of the cranial and mandibular anatomy of *Diatomys* that were either missing or obscured by postmortem deformation in previously described specimens of this species. IVPP V12692 shows that the infraorbital foramen of *Diatomys* is very large; hence, *Diatomys* resembles *Laonastes* (Fig. 1D) in having the hystricomorphous condition. IVPP V12692 also shows that the mandible lacks a coronoid process and has a relatively low condyle; the masseteric fossa extends forward to a level below p4; an anteroposterior ridge, the linea obliqua, separates dorsal and ventral portions of the masseteric fossa; the angular process is in the same vertical plane as the incisor (the sciurognathous condition); the angular process extends posteriorly as far as the condylar process; the ventral side of the angular process is very slightly inflected; and the incisor root is short, extending posteriorly to a level below m2. Thus, the new specimen demonstrates that the mandibles of *Diatomys* and *Laonastes* are virtually identical in sharing the following derived characters: absence of a coronoid process, masseteric fossa extending forward to below p4, masseteric fossa subdivided into dorsal and ventral sections, condyle low but higher than tooth row, and shortened incisor.

Laonastes was originally described as having a hystricognathous mandible (*2*). A reexamination of pertinent specimens shows that *Laonastes* actually has a sciurognathous mandible like that of *Diatomys* (Fig. 1, D and G). Another characteristic of hystricognathous rodents was also attributed to *Laonastes* in the original description: a groove for passage of the pars reflexa of the masseter superficialis muscle to its insertion on the medial surface of the angle. Reexamination of specimens of *Laonastes* revealed no space for this groove in its sciurognathous jaw.

Only heavily worn teeth of *Laonastes* are currently available for investigation. Nevertheless, the cheek teeth of *Laonastes* are clearly bilophodont, a condition that also characterizes *Diatomys*. The acquisition of bilophodonty occurred within Diatomyidae, because Oligocene species of *Fallomus* have cuspate cheek teeth showing derivation of the bilophodont pattern from a more generalized rodent dental morphology (*4*, *7*, *8*). The cheek teeth of *Laonastes* have elongated crowns that have been described as hypsodont. A highly unusual aspect of the dentition that *Laonastes* shares with fossil diatomyids is the presence of supernumerary roots on the cheek teeth. In *Laonastes*, the upper cheek teeth each have three roots, but their size and disposition are unusual for rodents. The upper cheek teeth of *Laonastes* bear an enlarged U-shaped anterior root and two posterior roots, whereas the lower dentition shows that three roots are present on p4 and four occur on m1-3 (Fig. 1F). In *Diatomys*, the upper molars each have four roots, whereas the number of roots supporting the lower dentition is identical to that of *Laonastes* (*3*, *5*). Molars of *Fallomus* exhibit some variation in the number of

[1]Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213, USA. [2]Laboratoire de Paléontologie, Institut des Sciences de l'Évolution, Case Courrier 064, Université Montpellier II, place Eugène Bataillon, F-34095 Montpellier Cedex 05, France. [3]Institute of Vertebrate Paleontology and Paleoanthropology, Post Office Box 643, Beijing 100044, People's Republic of China.

*To whom correspondence should be addressed. E-mail: dawsonm@carnegiemnh.org

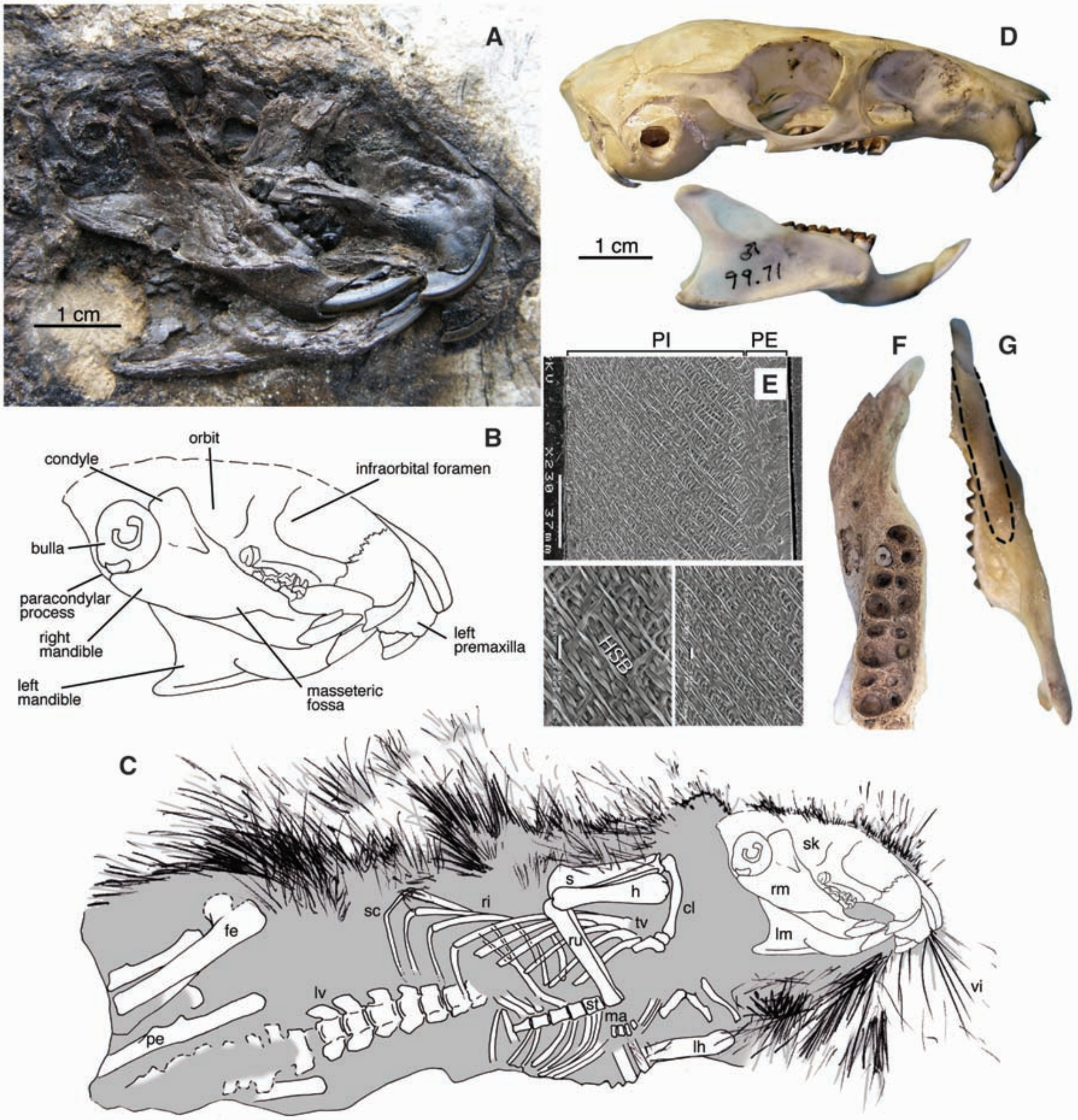

Fig. 1. Morphological characters of *Diatomys* and *Laonastes*. (**A** and **B**) Right side of skull and (**C**) articulated skeleton of *D. shantungensis* (IVPP V12692) from the early Miocene, Shandong Province, China. Abbreviations on the skeleton are as follows: cl, clavicle; fe, femur; h, right humerus; lh, left humerus; lv, lumbar vertebrae; ma, manus; pe, pelvis; ri, ribs; ru, right ulna; s, scapula; sc, sternal cartilage; sk, skull; st, sternum; tv, thoracic vertebrae; and vi, vibrissae. (**D** to **G**) *L. aenigmamus.* (D) Right lateral view of skull and mandible of specimen BMNH 1999.71. (E) Scanning electron photomicrographs of lower incisor enamel of BMNH 1998.407, showing the multiserial condition. (Top) Longitudinal section including the total enamel thickness (~310 μm) with moderately thin radial enamel of the portio externa (PE) and thick (80%) portio interna (PI) with HSBs; the straight HSBs are inclined at about 50° to the enamel-dentine junction at right; scale bar, 100 μm. (Bottom) Details of the PI, showing decussating HSBs with three to four prisms per band and the well-marked transition zone between adjacent decussating HSBs; a thin interprismatic matrix (IPM) never surrounds the prisms but appears as inter-row sheets running at a high angle (≥80°, nearly rectangular) to the prism direction and never anastomoses between the prisms; scale bars, 10 μm. The pattern of the IPM typifies a derived multiserial subtype III. (F) Occlusal view of left mandible of BMNH 1998.408, showing three roots of p4 and four roots of lower molars. (G) Ventral view of sciurognathous left mandible of BMNH 1999.71, with a dashed line showing the position of the lower incisor.

roots, but they typically have four (*7*). This proliferation of roots is derived among rodents, in which the primitive condition has three roots on P4-M3 (including two buccal roots and one larger lingual root) and two roots (one anterior and one posterior) on p4-m3. Given that four roots support the upper cheek teeth of *Diatomys* and *Fallomus*, the enlarged U-shaped anterior root on the upper cheek teeth of *Laonastes* probably resulted from the coalescence of the two anterior roots that occur in fossil diatomyids.

The microstructure of incisor enamel in *Fallomus* and *Diatomys* is multiserial, a condition that also characterizes ctenodactylid, pedetid, and hystricognath rodents (*5*, *8*). Although the original description of *Laonastes* failed to consider this character, our analysis of incisor enamel microstructure in *Laonastes* revealed the presence of multiserial enamel in this taxon as well (Fig. 1E). Incisor enamel microstructure in *Laonastes* is very similar to that of *Diatomys* in having the same number of prisms per Hunter-Schreger band (HSB) and in showing the same degree of complexity of the interprismatic matrix (inter-row sheets running at a high angle to the prism direction and a well-marked transition zone between adjacent decussating HSBs). It differs, however, in showing the HSBs to be much more inclined (>50°) to the enamel-dentine junction than is the case in *Diatomys* (25° to 30°), a difference that is not unexpected given the large temporal gap between these genera.

Other skeletal similarities between extinct diatomyids and *Laonastes* can be added to those of the mandible and dentition. *Laonastes* has a separate neurovascular canal within the orbit. This feature is not interpretable in available specimens of *D. shantungensis*, but the Oligocene *Fallomus* also has a separate neurovascular canal, demonstrating early establishment of this character in diatomyids (*7*). *Diatomys* and *Laonastes* are the same size, with head and body length spanning roughly 250 mm, followed by a long tail composed of 20 to 25 caudal vertebrae.

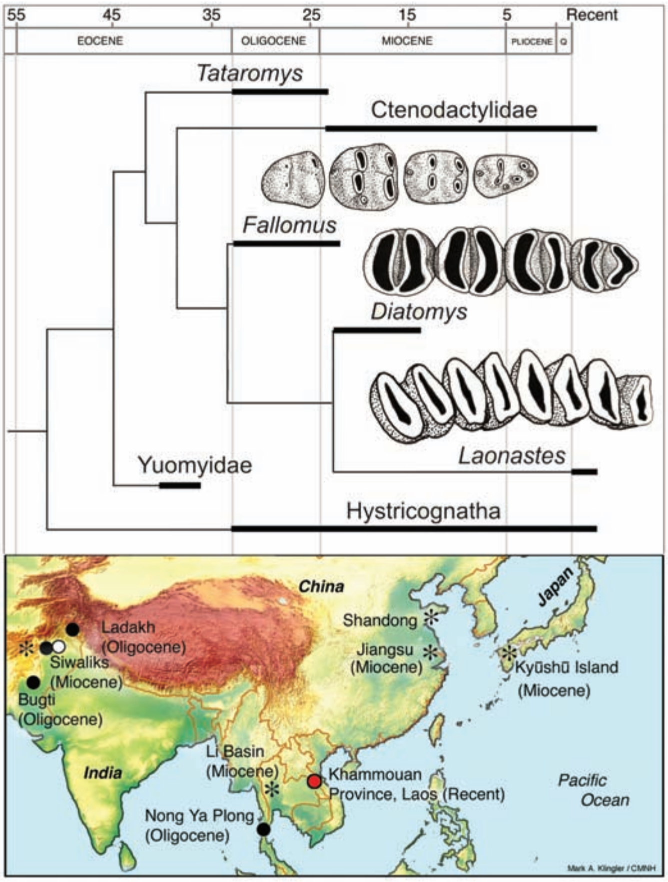

Fig. 2. Simplified phylogeny (see supporting online material) showing temporal and geographic distributions of diatomyids. (**Top**) Suggested relationships of diatomyids within Rodentia, showing occlusal views of right p4-m3 (anterior end to right) of *Fallomus*, *Diatomys*, and *Laonastes*. (**Bottom**) Geographic distribution of *Fallomus* (black circles), *Diatomys* (asterisks), *Willmus* (white circle), and *Laonastes* (red circle).

Diatomys and *Laonastes* also share the following postcranial characters: the humerus has a reduced deltoid ridge and a wide distal end and lacks an entepicondylar foramen; the lesser trochanter of the femur is mostly posterior in position; and the astragalus has a sharp medial keel, wide body, and short neck (*2*, *3*, *5*). Our phylogenetic analysis of morphological data from various living and extinct rodents identifies *Laonastes* as a member of Diatomyidae, being more closely related to *Diatomys* than the latter is to *Fallomus* (Fig. 2 and supporting online material). We therefore synonymize Laonastidae with Diatomyidae (*11*).

The discovery of the living diatomyid rodent *Laonastes* offers a rare opportunity to compare phylogenetic results that were derived independently from neontological and paleontological data sets. To date, phylogenetic analyses of genetic data from *Laonastes* have yielded conflicting results, but a combined analysis of mitochondrial data from 12*S* ribosomal RNA and cytochrome b places *Laonastes* as a basal member of Hystricognathi (*2*). Further molecular analyses should be undertaken, especially in light of the antiquity of the phylogenetic branching events postulated here for this rodent. A recent analysis of morphological data recognized diatomyids as one of several extinct outgroups of living Hystricognathi (*12*). Of these outgroups, it is striking that the diatomyids continued to evolve in Asia, while the ctenodactylids became extinct in southern Asia but evolved subsequently in Africa. Given the diversity of extinct Asian rodents that apparently lie near the base of the modern radiation of Hystricognathi, *Laonastes* strengthens paleobiogeographic hypotheses proposing that this group of mainly African and South American extant rodents originated in Asia (*6*).

The "Lazarus effect" refers to the reappearance of taxa after a lengthy hiatus in the fossil record (*13*, *14*). The discovery of living examples of taxa that were previously thought to be extinct is a very special case of the Lazarus effect, one that has only rarely been documented among mammals and other vertebrates. With the exception of microbiotheriid marsupials (*15*), all fossil mammal taxa that were subsequently found to be alive have been Pleistocene in age and congeneric with their modern counterparts (*16*). Uniquely among placental mammals, *Laonastes* pertains to a clade (Diatomyidae) that was formerly believed to have been extinct for more than 11 million years. Diatomyids join tree shrews, flying lemurs, and tarsiers as examples of ancient and formerly wider-ranging mammalian taxa that are currently living with relictual distributions in southeast Asia.

From a paleontological and phylogenetic perspective, efforts to conserve *Laonastes*, the sole survivor of a morphologically distinctive family of rodents with deep evolutionary roots in Asia, should be given the highest priority. If it can be preserved, the Paleogene zoo that survives today in southeast Asia can offer invaluable insights regarding past and present biodiversity.

References and Notes

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11. Synonymy: Diatomyidae (*5*) [including Laonastidae (*2*)]. Current content: type genus *Diatomys* (*3*), *Fallomus* (*4*), *Willmus* (*10*), and *Laonastes* (*2*). Range: early Oligocene to Recent, Asia. Diagnosis: rodents having hystricomorphous infraorbital foramen and sciurognathous mandible; mandible lacking coronoid process, condyle low but higher than cheek teeth, and masseteric fossa extending forward to below p4; dental formula 1/1, 0/0, 1/1, 3/3, with relatively large terminal teeth; upper incisor lacking groove; incisor enamel multiserial; supernumerary roots on cheek teeth; molar pattern varies from cuspate in early diatomyids to bilophodont; postcranial skeleton generalized. Differs from Ctenodactylidae in having large P4/4, supernumerary roots on cheek teeth, and a bilophodont occlusal pattern lacking loph/lophid connection between trigon/talon and trigonid/talonid; hypoconulids on lower cheek teeth are reduced to absent. Differs from bilophodont Geomyoidea in having hystricomorphous skull, multiserial incisor enamel, and large P4/4. Differs from bilophodont Pedetidae in having long, low skull and long lower jaw with low condyle, and lacking postcranial characters associated with bipedal locomotion.
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Supporting Online Material

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Materials and Methods
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Fig. S1
References

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