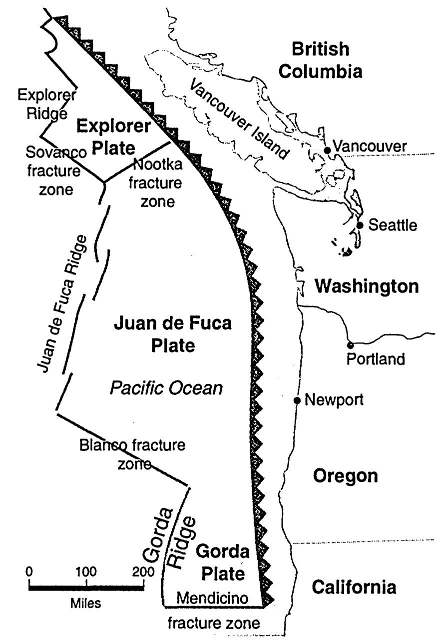
the locked fault is near the end of its stress buildup cycle, an episodic slip event may be sufficient to trigger a large earthquake (*8*).

The Cascadia slip episode, which took about 35 days, increased stresses across the shallower, earthquake-generating part of the plate boundary fault (white line segment in the figure on the previous page). This stress increase associated with the event is very small, equivalent to about half a year of steady stress buildup, bringing the fault very slightly closer to failure. The maximum change is about a factor of 10 smaller than the stress changes caused by earthquake slip that have triggered subsequent earthquake events (*9*).

The Cascadia subduction zone last experienced a great earthquake in 1700 (*10*) and so may be only about halfway through its ~600-year earthquake cycle. Therefore, even events substantially larger than the 1999 aseismic slip episode may not soon push this fault over the brink. However, other regional faults may be closer to failure and such episodic events could lead to large earthquakes. Continuous monitoring of these faults, in Cascadia and elsewhere, is thus of major importance.

Much remains to be learned about earthquake stress buildup. We do not yet know whether aseismic episodes are rare or common, large or small. For earthquakes, the numbers of events increases roughly tenfold for each unit decrease in earthquake magnitude. For aseismic events, we must determine the relation between frequency of occurrence, slip, and slipped area to understand what causes them and evaluate whether such episodes will trigger large earthquakes. For the Cascadia episode, the ratio of fault slip to fault area was quite small, about two orders of magnitude less than that typical for earthquake slip. This ratio is proportional to the stress change caused by the event, so the magnitude of the effects like those shown in the figure is less important when the ratio is small.



The Cascadia subduction zone. Subdiction of the Juan de Fuca plate beneath the North American plate results in the formation of the Cascade Range.

Recent work (*1*, *4*–*6*) has revealed a rich spectrum of aseismic behavior in seismically active regions but has also raised many new questions. Further progress in understanding these processes depends on the deployment of dense networks. Focused instrument clusters are needed to spatially resolve buried sources of deformation, many of which could be much smaller or more localized than that identified with the relatively sparse array used by Dragert *et al.* These arrays should also include ultrastable borehole strain meters, which are increasingly more sensitive than continuous GPS for time intervals of a month or less. Parallel developments are needed in refining analysis and modeling techniques aimed at extracting the maximum information from these large data sets (*11*).

Local prototype arrays of continuous GPS and borehole strain meters have recently been installed by the U.S. Geological Survey at Parkfield on the central San Andreas fault and at Long Valley caldera, a region of volcanic unrest in eastern California. Additional clusters in a range of geological environments will ensure timely acquisition of the kinds of data needed to capitalize on the capabilities of continuous GPS and borehole strain meter technology and rapidly expand our understanding of how earthquakes occur and why volcanoes erupt.

References and Notes

1. H. Dragert, K. Wang, T. K. James, *Science* **292**, 1525 (2001).
2. B. F. Atwater *et al.*, *Earthquake Spectra* **11**, 1 (1996).
3. P. Fluck, R. D. Hyndman, K. Wang, *J. Geophys. Res.* **102**, 20539 (1997).
4. A. T. Linde *et al.*, *Nature* **383**, 65 (1996).
5. K. Heki, S. Miyazaki, H. Tsuji, *Nature* **386**, 595 (1997).
6. S. Ozawa, M. Murakami, T. Tada, *J. Geophys. Res.* **106**, 787 (2001).
7. Aseismic slip occurs over a single discrete fault surface; ductile shearing is distributed over a tabular volume of rock.
8. W. Thatcher, *Nature* **229**, 12 (1982).
9. R. S. Stein, *Nature* **402**, 605 (1999).
10. K. Satake, K. Shimazaki, Y. Tsuji, K. Ueda, *Nature* **378**, 246 (1996).
11. P. Segall, M. Mathews, *J. Geophys. Res.* **102**, 22391 (1997).

PERSPECTIVES: PALEONTOLOGY

Digging Up Fresh Clues About the Origin of Mammals

André Wyss

The last two decades have been exhilarating for paleontologists and evolutionary biologists seeking to unravel phylogenetic relationships among living and extinct mammals. Stunning fossils have been unearthed from key locations worldwide and new methods have facilitated the comparison of these fossils with their living counterparts. The fossil reported by Luo *et al.* (*1*) on page 1535 of this issue is the latest gem in this string of paleontological pearls. They describe a beautifully preserved skull of a new synapsid taxon called *Hadrocodium* (synapsids are the group of legged vertebrates to which mammals belong), unearthed from the famous Early Jurassic (~195 million years old) Lufeng deposits of Yunnan Province in China.

Although the last 65 million years of Earth history (the Cenozoic Era) are often regarded as "the age of mammals," the major branches of the mammalian evolutionary tree diverged tens of millions of years earlier, during the Mesozoic Era (see the figure). We have known about fossils of Mesozoic mammals for about 200 years. But it is only recently that significant numbers of reasonably complete skulls and skeletons have become available. Prior to this, information was limited to what could be gleaned from skeletal bits and pieces, such as teeth and jaw fragments. Indeed, much of our knowledge about mammalian evolution stems from analyses of the highly specialized teeth for which mammals are noted. The availability of exquisitely preserved skulls and skeletons of many early mammalian lineages has diminished the influence of this tooth-centric perspective, leading to the emergence of a highly integrated understanding of mammalian phylogeny.

A consideration of the outwardly undemanding question "How old is the oldest mammal?" reveals one recent improvement in the naming of groups of organisms. Traditionally, formal taxonomic names, such as Mammalia, have been equated with "key" or "defining" morphological traits—for example, mammary glands, hair, or a dentary-squamosal jaw

The author is in the Department of Geological Sciences, University of California, Santa Barbara, CA 93106, USA. E-mail: wyss@geology.ucsb.edu

articulation (*2*). This practice has led to generally futile debates about which characteristics are "defining" features, and endless wrangling about where the mammal/nonmammal "boundary" should be placed. The scientific meaning of taxonomic names, however, is increasingly viewed as deriving entirely from clear linkages of those names to particular groups of organisms (*3*). The issue thus reduces to one of choosing which branch of the synapsid evolutionary tree to link with the name Mammalia.

Overwhelming evidence points to the divergence of monotremes (the egg-laying platypus and echidna) and therian mammals (marsupials and placentals that give birth to live young) from a unique common ancestor. Robust evidence for this shared heritage is not surprising given that both monotremes and therians have living representatives, and so are amenable to a much wider range of comparisons than are possible with fossil remains. Most scientists who study synapsids work on living forms, that is, members of a branch of the evolutionary tree that includes the most recent common ancestor of monotremes and therians plus all of its descendants. Thus, it is expedient to assign the name Mammalia to this branch; among other benefits, this ensures that this name will be used equivalently by paleontologists studying fossils and biologists studying living representatives (*2*).

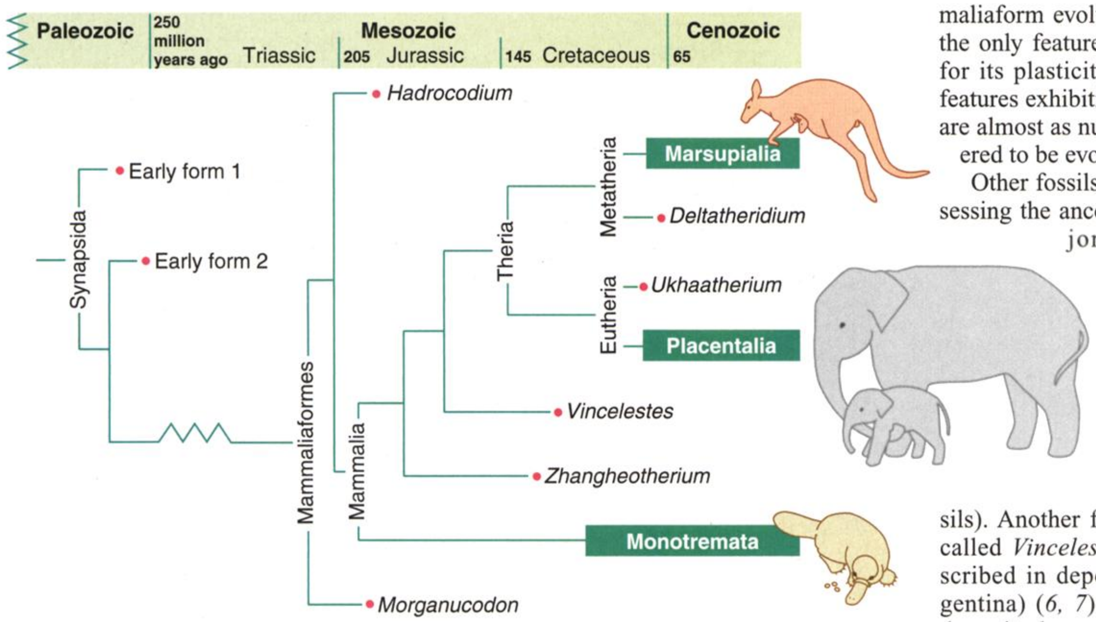
The new fossil, *Hadrocodium*, is distinctive in numerous ways, perhaps the most striking of which is its exceedingly small size (its estimated body mass is about 2 g). Meticulous anatomical and phylogenetic analyses by Luo and colleagues reveal that *Hadrocodium* diverged before the appearance of the most recent common ancestor of monotremes and therians. So, strictly speaking, it is not a mammal, but is a member of the Mammaliaformes—a broader grouping comprising mammals and some of their closest fossil allies. However, as the nearest securely identified relative of mammals, *Hadrocodium* has proved uniquely valuable for documenting the sequence of morphological changes that led to the emergence of mammalian ancestors. If it were not for the synapsid fossil record, we would know only that myriad evolutionary novelties—such as three middle ear bones and a lower jaw composed of a single bone—appeared sometime before the divergence of monotremes and therians, and sometime after the divergence of mammals and their nearest living relatives, the reptiles. Instead, from analyses of *Hadrocodium* and many other fossils, we have a detailed understanding of the long sequence of changes that resulted in these unique structures.

Hadrocodium is firmly positioned as the nearest fossil relative of mammals, thereby clarifying which morphological features are ancestral for Mammalia. Besides three middle ear bones and a single jaw bone, *Hadrocodium* shares other evolutionarily unique features with mammals, such as an advanced configuration of the secondary palate and an elevated and anteriorly shifted craniomandibular (jaw) joint.

Another intriguing feature of *Hadrocodium* is its cranium, which is enormous compared to those of its contemporaries. Remarkably, mammaliaforms exhibit a huge range in cranium volume (relative to skull width). This wide variation evinces the plasticity of this feature among mammaliaforms and the considerable evolutionary convergence (or reversal) associated with cranial enlargement during mammaliaform evolution. This is by no means the only feature of mammaliaforms noted for its plasticity. In fact, mammaliaform features exhibiting convergence or reversal are almost as numerous as features considered to be evolutionarily more stable (*4*).

Other fossils have been valuable for assessing the ancestral morphologies of major subgroups within the Mammalia. A nearly complete skeleton of a close relative of Theria, *Zhangheotherium* (*5*), has been unearthed from deposits in Liaoning Province, eastern China (also celebrated for their feathered dinosaur fossils). Another fossil predating the Theria, called *Vincelestes*, has recently been described in deposits from Patagonia (Argentina) (*6*, *7*). Finally, Late Cretaceous deposits have produced spectacular remains assigned to taxa that represent the nearest relatives of placental and marsupial therians, *Ukhaatherium* (*8*) and *Deltatheridium* (*9*), respectively. These two fossils are shedding much needed light on the divergence of the two dominant subgroups of modern mammals.

The welcome discovery of the tiny but crucial fossil of *Hadrocodium* demonstrates yet again the continued handsome scientific payoffs that emerge from the time-honored practice of hunting for ancient bones.



Honoring the ancestors. Simplified branching diagram of the phylogenetic relationships among the major groups of living mammals and their fossil relatives. Taxonomic names associated with various branches are shown. Extant groups are indicated by dark green boxes. Divergence times for more inclusive branches are estimated.

References

1. Z.-X. Luo *et al.*, *Science* **292**, 1535 (2001).
2. K. de Queiroz, *Syst. Biol.* **43**, 497 (1994).
3. K. de Queiroz, J. Gauthier, *Syst. Biol.* **39**, 307 (1990).
4. Q. Ji, Z. X. Luo, S. A. Ji, *Nature* **402**, 898 (1999).
5. Y. M. Hu, Y. Q. Wang, Z. X. Luo, C. K. Li, *Nature* **390**, 137 (1997).
6. J. F. Bonaparte, G. W. Rougier, in *Actas IV Congreso Latinoamericano de Paleontologia, Bolivia 1* (1987), p. 343.
7. G. W. Rougier, thesis, Universidad Nacional de Buenos Aires (1993).
8. M. J. Novacek *et al.*, *Nature* **389**, 483 (1997).
9. G. W. Rougier, J. R. Wible, M. J. Novacek, *Nature* **396**, 459 (1998).