control chambers from both fields were averaged together in the same fashion. All emissions data are "net emissions," as both production and consumption of methyl halides may occur in the sample chamber.

19. Methyl bromide and methyl iodide background concentrations, taken at 1 meter height, showed marked increases from early season concentrations of 12 and 2 pptv (parts per trillion by volume). Methyl bromide concentrations of 20 to 50 pptv were observed for the last 2 months of the season, and a prolonged increase in methyl iodide concentrations (30 to 200 pptv) was measured during the early to midseason.
20. The bromide content in the Japanese fields is 0.7 and 1.1 mg/kg dry weight, respectively, and emissions from these fields are 3.7×10^{-6} and 5.8×10^{-6} g m^{-2} day^{-1} for the listed bromide concentrations. The chloride ion concentration in the Japanese fields was 120 to 450 mg/kg dry weight. Observed emissions of methyl chloride in Japan were 5.8×10^{-5} and 1.5×10^{-4} g m^{-2} day^{-1}.
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29. Methyl chloride emissions from control plots were very similar to emissions from planted plots. When extrapolating using global rice-field area, control plot emissions are equivalent to 4.1 Gg/year. When the global wetland area of 3.56×10^{12} m^2 is used, extrapolated emissions of methyl chloride are 10.1 Gg/year. These emissions may be due to a process similar to that responsible for emissions of methyl chloride in fens and salt marshes.

30. We thank the owners and operators of Canal Farms in Maxwell, CA; C. van Kessel, who provided lab space and equipment; the lab of K. Scow, including J. Macalady, A. Dickens, and E. Burton, for aid in gas sample collection, methane analysis, and field-site maintenance; M. Hair for field advice; H. Ajie and K. Yagi for help with gas sample collection; and A. Gotoh for gas collection and field equipment tests. Supported by NSF grant ATM-9731706, USDA grant 58-3148-7-085, and USDA award 9900921.

5 June 2000; accepted 25 September 2000

Early Permian Bipedal Reptile

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A 290-million-year-old reptilian skeleton from the Lower Permian (Asselian) of Germany provides evidence of abilities for cursorial bipedal locomotion, employing a parasagittal digitigrade posture. The skeleton is of a small bolosaurid, *Eudibamus cursoris*, gen. et sp. nov., and confirms the widespread distribution of Bolosauridae across Laurasia during this early stage of amniote evolution. *E. cursoris* is the oldest known representative of Parareptilia, a major clade of reptiles.

During the Late Pennsylvanian–Early Permian, terrestrial tetrapods diversified greatly and adapted to a broad array of herbivorous and predatory modes of life (*1*). Yet even the most advanced terrestrial amniotes of this time exhibit skeletal features that are indicative of awkward, relatively slow locomotion, such as massive girdles, short stocky limbs, and a "sprawling" posture and gait. We report here on the discovery of a small, nearly complete skeleton of an Early Permian reptile whose skeletal anatomy indicates a capability to attain relatively high speeds during bipedal and quadrupedal locomotion using a parasagittal gait and digitigrade stance. This reptile precedes bipedal parasagittal archosaurs (including dinosaurs) by at least 60 million years.

E. cursoris gen. et sp. nov. (*2*) is part of a recently collected diverse assemblage of fully terrestrial tetrapods from the Lower Permian of central Germany, near the village of Tambach-Dietharz, Thuringia (*3*). *E. cursoris* is referred to the rare, poorly understood taxon Bolosauridae, which includes *Bolosaurus striatus* from the Lower Permian of Texas (*4*), *Belebey vegrandis* and *B. maximi* from the Upper Permian of Russia (*5*), and evidence of bolosaurid remains from the Upper Permian of China (*6*). Until now, however, bolosaurids were known almost exclusively by their skulls because postcrania were limited to a few vertebrae and incomplete limb and girdle elements of *Bolosaurus* (*4*).

The holotype and only known specimen of *E. cursoris* consists of a nearly complete skeleton, with only a few elements of the skull, forelimb, and the tip of the tail being either missing or incompletely represented (Fig. 1). The skull is partially disarticulated but clearly possesses several bolosaurid characters. Most prominent is a long, low, temporal opening bordered dorsally by the jugal and squamosal and ventrally by the quadratojugal. Only a small remnant of the latter bone is preserved, projecting anteriorly from the ventral margin of the left squamosal. A long, narrow, boomerang-shaped postfrontal wraps around the posterodorsal margin of the orbit. As in other bolosaurids, the palate is devoid of teeth, and the greatly reduced transverse flange of the pterygoid lies in the same plane as the palate proper. In the lower jaw, as in other bolosaurids, the dentary and surangular form a high, broad-based coronoid process, and a medial lamina of the dentary extends nearly to the ventral margin of the jaw and is covered by a long anterior extension of the prearticular. The upper and lower marginal dentition exhibits the highly unusual bolosaurid structure of bulbous occluding teeth that is considered indicative of high-fiber herbivory (*7*).

The postcranial skeleton of *E. cursoris* has 26 presacral vertebrae with broadly swollen neural arches and very slender, short ribs. The unusual length of the tail, which includes 55 preserved vertebrae, is due to an elongation of the midregional and posterior elements. The appendicular skeleton has a combination of proportional and structural features that is strongly persuasive of an ability to run not only bipedally but with the hindlimbs held in a nearly erect vertical position and swung in a pendulumlike parasagittal arc, with the pes assuming a digitigrade posture. This form of locomotion is unique among Paleozoic tetrapods. It has been generally accepted that the first appearance of the initial stages of parasagittal limb orientation occurred in the Early Triassic archosaurian antecedents of dinosaurs and crocodilians, whereas the achievement of a fully erect limb posture and parasagittal bipedalism is first documented in the Late Triassic saurischian and ornithischian dinosaurs (*8*). On the other hand, the earliest appearance of bipedalism without the abandonment of the primitive "sprawling" posture and gait may have occurred in the Late Permian lepidosaurian reptiles (*9*) and was retained or independently acquired in many modern lizard lineages (*10–13*). Thus, *Eudibamus* was apparently the earliest known tetrapod capable not only of facultative bipedalism but also of using its hindlimbs primarily in a parasagittal plane with the pes in a digitigrade posture during rapid locomotion (Fig. 2).

The evidence of bipedalism in *Eudibamus* is based principally on specialized skeletal proportions that are not only associated with facultatively bipedal locomotion in modern lizards (*10–12*, *14*, *15*) but also characterize fully bipedal dinosaurs that used a parasagittal gait (*16*). Most compelling are the rela-

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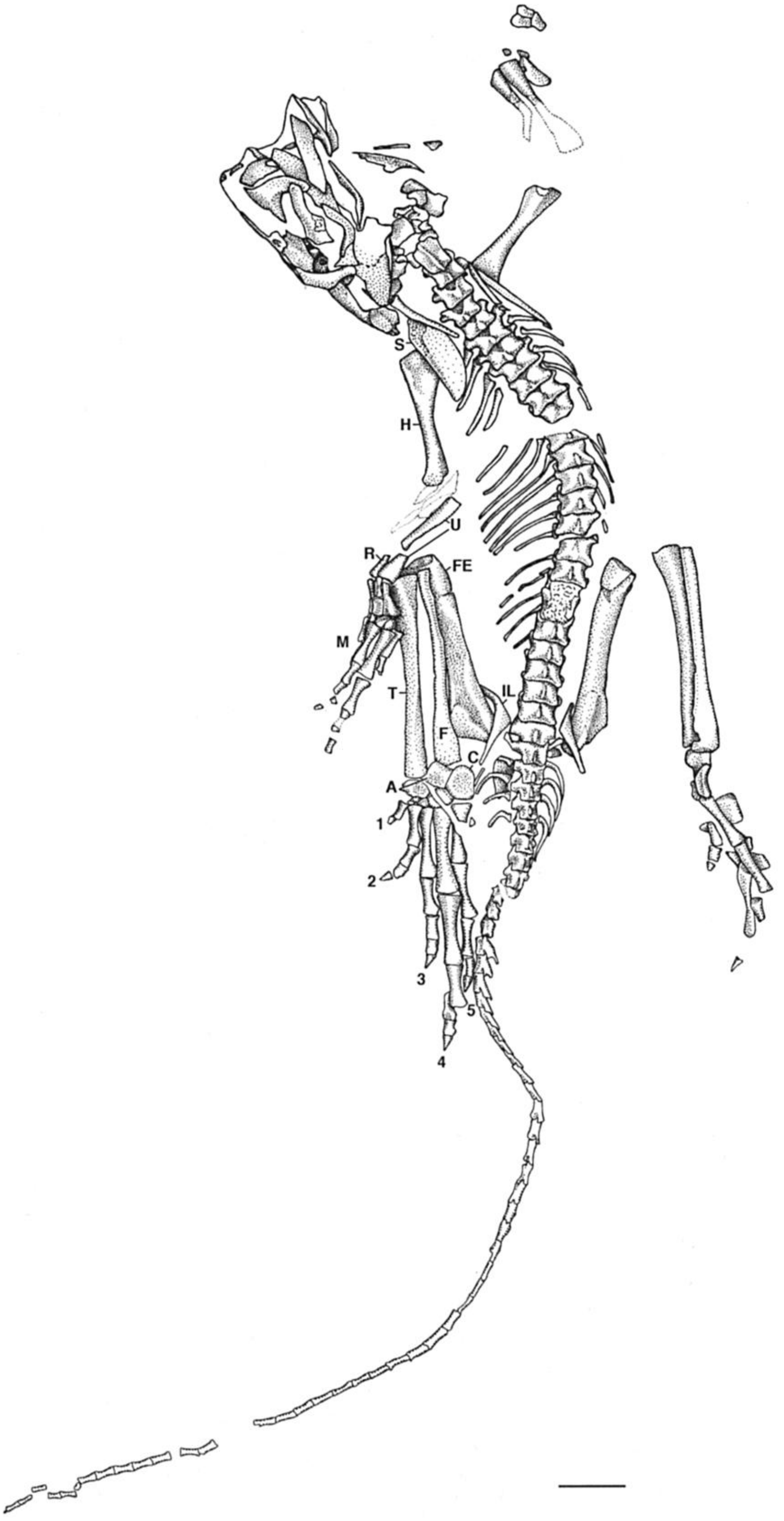

Fig. 1. Skeleton of *E. cursoris* gen. et sp. nov. (MNG 8852). The skeleton (total measured length = 261.5 mm) has been preserved with little or no distortion. The skull, although complete, has partially disarticulated, and a crack associated with collecting this small delicate skeleton passes through the pes, splitting the astragalus. Abbreviations: A, astragalus; C, calcaneum; F, fibula; FE, femur; H, humerus; IL, ilium; M, manus; R, radius; S, scapula; U, ulna; 1 through 5, digit numbers. Scale bar = 1 cm.

tively short forelimb as compared to the hindlimb and the relatively long hindlimb and tail as compared to the trunk. The values for the length ratios expressing these features in *Eudibamus* approach closely or even surpass those in modern lizards that are recognized as facultatively bipedal specialists (*Basiliscus* and *Crotaphytus*), but they contrast sharply with those of representative Paleozoic and Triassic amniotes (Table 1).

Relative shortening of the forelimb is traditionally explained as a result of its having a decreasing role in rapid locomotion, particularly in bipedal forms. However, bipedalism in lizards may not necessarily provide speed or acceleration advantages over quadrupedal locomotion. Rather, the disuse of the forelimbs during rapid running may be to avoid interference with the long-striding hindlimbs or because of an inability of the shorter forelimbs to match the velocities of the hindlimbs (*13*, *15*). The lengthening of the hindlimb, however, can only be explained as serving to increase speed by lengthening the stride (*10*, *12–14*, *15*). Regardless of the type of limb posture used, it is by increasing stride length and not stride frequency that running speeds are most greatly increased and sustained in bipedal and quadrupedal locomotion (*12*, *13*, *15*). The enormous relative length of the hindlimb in *Eudibamus* obviously involved all of the long bones (Fig. 3). Although the femur and crus are subequal in length, the pes is especially long, as indicated by the unusually great relative length of the fourth digit. This suggests a potentially great stride length and speed, particularly when compared to Paleozoic contemporaries. In bipedal lizards, the pes length rather than the total limb length may be a more important dimension for relating limb structure to maximum attainable speeds (*15*). Direct observations reveal that lizards frequently rely more on digitigrade foot posture than on full vertical extension of the upper limb to increase stride length with the attainment of maximum locomotor performance (*13*, *15*). Whereas the primitive, reptilian relative length pattern of the metatarsals to each other is retained in *Eudibamus*, the extraordinary relative increase in the length of the pes is accomplished by a lengthening of digits 3 through 5. Reptiles exhibiting arboreal, clinging, and leaping behaviors also possess relatively elongate hindlimbs and tails. This interpretation for *Eudibamus* is rejected, however, as it does not display the elongate penultimate phalangeal elements typically associated with such animals (*17*).

The long tail would have provided ample space for caudofemoral limb retractor musculature. Its overall mass would not only have kept the center of gravity close to the hip joint but would also have been able to compensate for changes in the center of gravity during bipedalism (*10*, *11*).

Arguments for a near vertical parasagittal gait of the hindlimb in *Eudibamus* are based on numerous characteristics that duplicate or mimic features typically associated with forms considered uncontrovertibly to use this sort of locomotion. The articular facets at the knee and ankle indicate that when the hindlimb was fully extended, the long axes of the long bones could only be aligned closely with each other and are contained approximately in a single plane during flexion-extension at the knee and ankle joints. These restrictions would be expected only if the limb were held in a nearly vertical position while swung pendulum-style in a near parasagittal plane during locomotion. The crurofemoral facets are flat and terminal and occupy a plane that is nearly perpendicular to the long axis of the extended limb. This is in contrast to three features of the distal end of the femur that are consistently associated with sprawling-type vertebrates (*18*): (i) an asymmetrical development in size and shape of the distal femoral condyles, with the posterior or lateral condyle being larger and more distally elongated than the anterior or medial condyle; (ii) articulation of the fibula with the posterolateral surface of the posterior or lateral condyle; and (iii) the positioning of the articular facets for the tibia primarily on the ventral surface of the condyles. A similar set of features of the elbow joint is also present in Paleozoic sprawlers (*19*). The result is an asymmetrical hinge-type joint that effects a partial rotation of the epipodials about their long axis, so that the dorsal surfaces face forward, and confines the flexion of the epipodials to a parasagittal plane during limb protraction (*18*).

Other unusual features of the hindlimb and pes of *Eudibamus* can be explained as adaptations to parasagittal locomotion. The upper limb elements are straight and slender, with little separation between the epipodials, and exhibit little expansion of the proximal and distal heads. The tarsus exhibits a considerable degree of compactness, with a tight union between the proximal (astragalus and calcaneum) elements and loss of the perforating foramen, and the loss or reduction of several distal elements. Digits 3 through 5 exhibit a strong degree of bilateral symmetry with the unusual lengthening of digit 5 and compactness about the long axis of the limb. During maximum cursorial speeds, the pes almost certainly assumed a digitigrade posture, as presumed in bipedal dinosaurs and observed in modern bipedal lizards (*13*, *15*, *16*), and the relatively short digits 1 and 2 lost contact with the substrate. In contrast to forms highly adapted to a vertical limb posture and a parasagittal gait, the proximal head of the femur in *Eudibamus* is not distinct and is turned only slightly medially into the acetabulum. In contrast to Paleozoic tetrapods, however, the well-preserved head is extremely narrow, with only a slightly convex articulating facet, suggesting a large, probably rounded cartilaginous cap. This femoral design would have allowed for considerable freedom of orientation of the shaft. Furthermore, the massive internal trochanter is positioned far distally from the proximal head so as to not

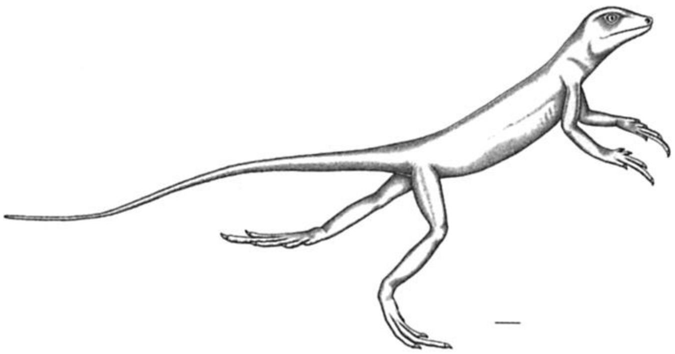

Fig. 2. Reconstruction of *E. cursoris* running at near maximum bipedal speeds, with hindlimbs held nearly vertical and foot posture digitigrade. The body posture is based in large part on studies of extant bipedal specialist lizards (*10*, *13*). The upper portions of the hindlimb and forelimb are foreshortened in order to account for the estimated 15° lateral tilt of the femur and humerus, respectively.

Table 1. Body proportions given as percentages for various fossil and extant reptiles as follows: *Eudibamus*; late Paleozoic captorhinomorphs *Paleothyris* (*22*) and *Captorhinus* (*23*); primitive diapsid *Petrolacosaurus* (*21*); primitive synapsid *Varanops* (*26*); Triassic archosauromorph *Euparkeria* (*27*); and extant lizards *Basiliscus*, *Crotaphytus*, and *Sceloporus* (*11*). Abbreviations for measured lengths are as follows: FL, forelimb; HL, hindlimb; T, tail; TA, total axial; TR, trunk; 4th DM, fourth digit of manus; 4th DP, fourth digit of pes.

	FL/TR	HL/TR	FL/HL	T/TA	4th DM/TR	4th DP/TR
Eudibamus	82.7	134.7	61.4	64.3	28.0	52.4
Paleothyris	45.2	62.5	72.4	–	22.3	32.3
Captorhinus	59.7	66.4	89.0	–	17.9	18.7
Petrolacosaurus	63.6	66.1	96.2	50.0	22.0	21.3
Varanops	57.4	65.0	88.5	57.1	26.1	22.4
Euparkeria	40.6	66.7	60.1	61.6	–	41.6
Basiliscus	49.4	105.3	46.9	71.4	16.5	41.7
Crotaphytus	50.2	96.6	51.9	64.7	17.2	39.1
Sceloporus	52.8	78.4	67.3	60.5	18.2	32.9

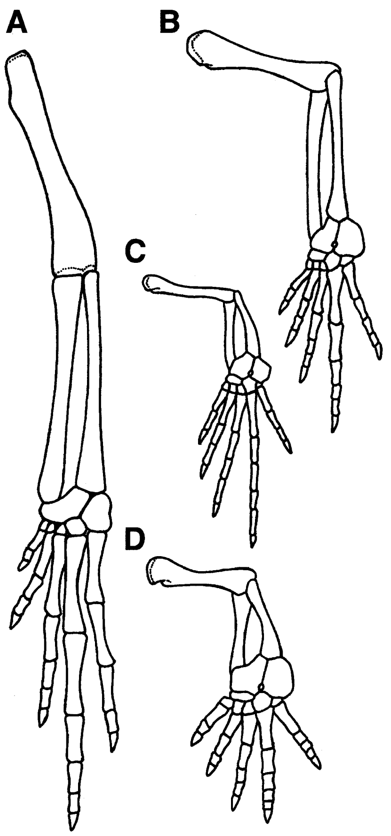

Fig. 3. Right hindlimbs in posterior view of (**A**) *E. cursoris* and the other relatively small, late Paleozoic reptiles (**B**) *Petrolacosaurus* (*21*), (**C**) *Paleothyris* (*22*), and (**D**) *Captorhinus* (*23*). All are scaled to individuals with identical trunk lengths to emphasize proportional size differences. The orientations of each limb relative to the vertical have been determined on the basis of various surfaces of articulation, but with the pes fully extended rather than in contact with the ground in order to show the total length of the limb. For example, the distal femoral articulation of (B) through (D) restricts the tibia and the fibula largely to the ventral and posterior surfaces of the femur, respectively, resulting in a sprawled posture. This is in strong contrast to the condition in *E. cursoris* (A), where both tibia and fibula attach to the terminal end of the femur. In addition, digits 3 through 5 in *E. cursoris* are held tightly together, parallel to the long axis of the limb, and digit 5 is greatly elongated, slightly exceeding the total length of digit 3 (see Table 1 for measurements).

limit the degree to which the femur can act in a vertical plane without contacting the pelvis. This contrasts with modern bipedal lizards in which the large trochanter is adjacent to and directly below the proximal head and would be forced against the ventral acetabular rim during adduction of the femur, levering the head from the socket (*10–12*, *14*). With increasing speeds during bipedal running in lizards, the femur may approach a vertical orientation at footfall, but this is accomplished by pelvic roll rather than by adduction (*15*). Although the acetabulum is not exposed in *E. cursoris*, a partial pelvis of *B. striatus* does show a strong dorsal acetabular rim that would have facilitated a near-vertical femoral orientation (*4*).

The forelimb of *Eudibamus* also possesses several features that can be interpreted as adaptations to parasagittal locomotion: (i) the humerus is elongate and slender but has retained a large deltopectoral crest, (ii) the carpus is compact, and (iii) the digits of the hand are greatly elongated. The overall elongation of the forelimb and manus indicate that *Eudibamus* was probably capable of parasagittal quadrupedal locomotion until speeds were reached that required bipedalism. As *Eudibamus* was herbivorous, based on the typical bolosaurid dental and mandibular morphology (*7*), it likely used sprinting speeds to escape predators.

Although small in size and mainly represented in the fossil record by fragmentary remains, bolosaurid parareptiles (Fig. 4) are unusual among amniotes in achieving a wide Laurasian distribution early in the Permian (*20*), which includes the United States, Germany, southern Russia, and China (*4–6*). Perhaps this precocious dispersal and early success were related to the unique combination of bipedalism and herbivory.

References and Notes

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23 August 2000; accepted 23 September 2000

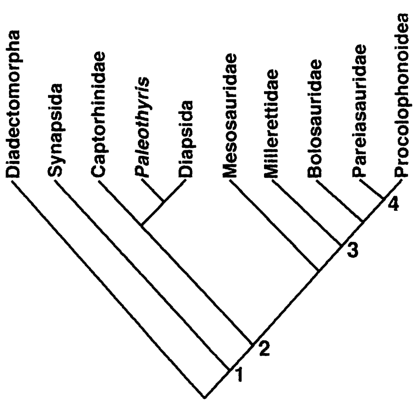

Fig. 4. Cladogram of Paleozoic amniotes, illustrating the single most parsimonious pattern of relationships from a PAUP version 3.1.1 analysis (D. Swofford, Laboratory of Molecular Systematics, Smithsonian Institution, 1993), based on previously published data matrices (*24*, *25*) except for the inclusion of bolosaurids. The tree length is 225 steps, with a consistency index of 0.809 and a retention index of 0.672. Major clades are designated as follows: 1, Amniota; 2, Reptilia; 3, Parareptilia; and 4, Procolophonia. It is the anatomy of *E. cursoris* that has allowed us to determine for the first time that bolosaurids are parareptiles and the sister taxon of Procolophonia. The high position of bolosaurids within parareptiles is unexpected, as the bolosaurids are the oldest known members of this clade, with a fossil record extending to the base of the Permian. However, this finding is consistent with recent phylogenetic data that indicate the presence of long ghost lineages for parareptiles (*25*).

A Kingdom-Level Phylogeny of Eukaryotes Based on Combined Protein Data

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Current understanding of the higher order systematics of eukaryotes relies largely on analyses of the small ribosomal subunit RNA (SSU rRNA). Independent testing of these results is still limited. We have combined the sequences of four of the most broadly taxonomically sampled proteins available to create a roughly parallel data set to that of SSU rRNA. The resulting phylogenetic tree shows a number of striking differences from SSU rRNA phylogeny, including strong support for most major groups and several major supergroups.

SSU rRNA sequences constitute the single most comprehensive database available for phylum-level systematics (*1–4*). These data depict the eukaryotes as a series of deeply diverging lineages branching successively toward a dense unresolved cluster [the so-called eukaryote crown (*5*)]. Because the latter include the majority of eukaryotes, this has led to suggestions that most major eukaryote taxa arose in a single explosive radiation (*5*, *6*), and, together with poor resolution in many protein-based phylogenies, to speculation that relationships among these taxa may never be resolved (*6*). Although phylogenies of protein genes and rRNAs often conflict, currently available protein data are plagued by uneven taxonomic sampling, wide disparities in evolutionary rates

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