

# Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization

Peter Ward\*<sup>†</sup>, Conrad Labandeira<sup>‡§</sup>, Michel Laurin<sup>¶</sup>, and Robert A. Berner<sup>†||</sup>

\*Department of Biology, University of Washington, Seattle, WA 98195; <sup>†</sup>Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012; <sup>‡</sup>Department of Entomology, University of Maryland, College Park, MD 20742; <sup>§</sup>Formations de Recherche en Évolution 2696, Centre National de la Recherche Scientifique, Université Paris 6–Pierre et Marie Curie, Two Place Jussieu, Case 7077, 75005 Paris, France; and <sup>||</sup>Department of Geology and Geophysics, Yale University, New Haven, CT 06520-8109

Contributed by Robert A. Berner, September 12, 2006

The first terrestrialization of species that evolved from previously aquatic taxa was a seminal event in evolutionary history. For vertebrates, one of the most important terrestrialized groups, this event was interrupted by a time interval known as Romer's Gap, for which, until recently, few fossils were known. Here, we argue that geochronologic range data of terrestrial arthropods show a pattern similar to that of vertebrates. Thus, Romer's Gap is real, occupied an interval from 360 million years before present (MYBP) to 345 MYBP, and occurred when environmental conditions were unfavorable for air-breathing, terrestrial animals. These model results suggest that atmospheric oxygen levels were the major driver of successful terrestrialization, and a low-oxygen interval accounts for Romer's Gap. Results also show that terrestrialization among members of arthropod and vertebrate clades occurred in two distinct phases. The first phase was a 65-million-year (My) interval from 425 to 360 MYBP, representing an earlier, prolonged event of complete arthropod terrestrialization of smaller-sized forms (425–385 MYBP) and a subsequent, modest, and briefer event of incipient terrestrialization of larger-sized, aquatic vertebrates (385–360 MYBP). The second phase began at 345 MYBP, characterized by numerous new terrestrial species emerging in both major clades. The first and second terrestrialization phases bracket Romer's Gap, which represents a depauperate spectrum of major arthropod and vertebrate taxa before a major Late Paleozoic colonization of terrestrial habitats.

atmospheric O<sub>2</sub> | Paleozoic | tetrapods

The pattern of terrestrialization by animals as recorded in the fossil record (1) indicates that arthropods, with species interpreted as fully land-based before 400 million years before present (MYBP) (2), preceded vertebrates onto land by tens of millions of years. The first body fossils identified as stegocephalians (limbed vertebrates) are known from strata ≈370 MYBP, such that the appearance of the limb with digits, the loss of the opercular apparatus, and the development of other characters that subsequently allowed a terrestrial lifestyle, presumably occurred during the 25-My interval between 385 and 360 MYBP (3, 4). Most of our understanding about these crucial vertebrate events comes from only a few freshwater deposits from Euramerican localities, with outcrops in Greenland producing the most prolific stegocephalian remains. *Elginerpeton* and *Obruchevichthys* were first, between 385 and 375 MYBP, followed several million years later by a modest radiation that included *Ventastega*, *Ichthyostega*, *Acanthostega*, *Tulerpeton*, *Metaxygnathus*, and *Hynnerpeton*. Although most of these taxa possessed limbs (although this is not certain for *Elginerpeton* and *Obruchevichthys*), all of these taxa have been interpreted as fully aquatic, rather than terrestrial (5–7). Their respiratory systems are poorly known, but osteology suggests that they were able to derive some amount of O<sub>2</sub> from water instead of being entirely air breathing (8). These stegoceph-

alians disappeared soon thereafter, followed rapidly by rare appearances of limbed vertebrates. This temporal gap has long been called Romer's Gap, and until recently it was unknown whether this hiatus was due to a combination of unfavorable taphonomic conditions and collection failure or whether it represented an interval of intrinsically low diversity and an abundance of limbed vertebrates. Romer's Gap separates occurrences of the earliest (Late Devonian) aquatic stegocephalians from a much larger adaptive radiation that included the first terrestrial vertebrates that commenced during the Viséan stage of the Early Carboniferous. Although new collections have partly filled Romer's Gap (9), including the discovery of the early limbed vertebrate *Pederpes*, our recent findings suggest that it is not collection failure that has resulted in this near absence of limbed vertebrate occurrences. Here, we test the hypothesis that Romer's Gap is accounted for by environmental factors by examining the ranges of terrestrial arthropods over the same time interval.

Until now there has been little attention to whether terrestrial arthropods also show an equivalent of Romer's Gap. Romer's Gap (10, 11) was a time designation heretofore applied only to the fossil record of stegocephalians, whose original definition is the one used herein. However, arthropodan data can provide new information and insight into environmental conditions during the Devonian to Carboniferous time interval.

## Results

The first terrestrialized macroscopic eumetazoans can be used to estimate standing diversity from 425 MYBP, just before the earliest arthropod fossils (2), to ≈280 MYBP (Fig. 1), the latter a time of recognized high diversity in both arthropods and terrestrial vertebrates (12, 13). For this interval we plotted the geochronologic ranges and standing diversities of major, terrestrialized early arthropod and vertebrate clades (Figs. 1 and 2). Clades for arthropods consisted of myriapods, arachnids and hexapods, whereas those for vertebrates comprised stegocephalians. Because of a great abundance of arthropod taxa, the origination rate of arthropod orders additionally was determined, based on taxonomic orders (Fig. 2). Also documented during this interval are wide fluctuations in atmospheric O<sub>2</sub> levels, shown in Fig. 1, that are defined in greater detail in Fig. 2.

A plot of the recently computed atmospheric O<sub>2</sub> levels against diversity data for major clades of arthropods and limbed verte-

Author contributions: P.W. designed research; P.W., C.L., M.L., and R.A.B. performed research; and P.W., C.L., M.L., and R.A.B. wrote the paper.

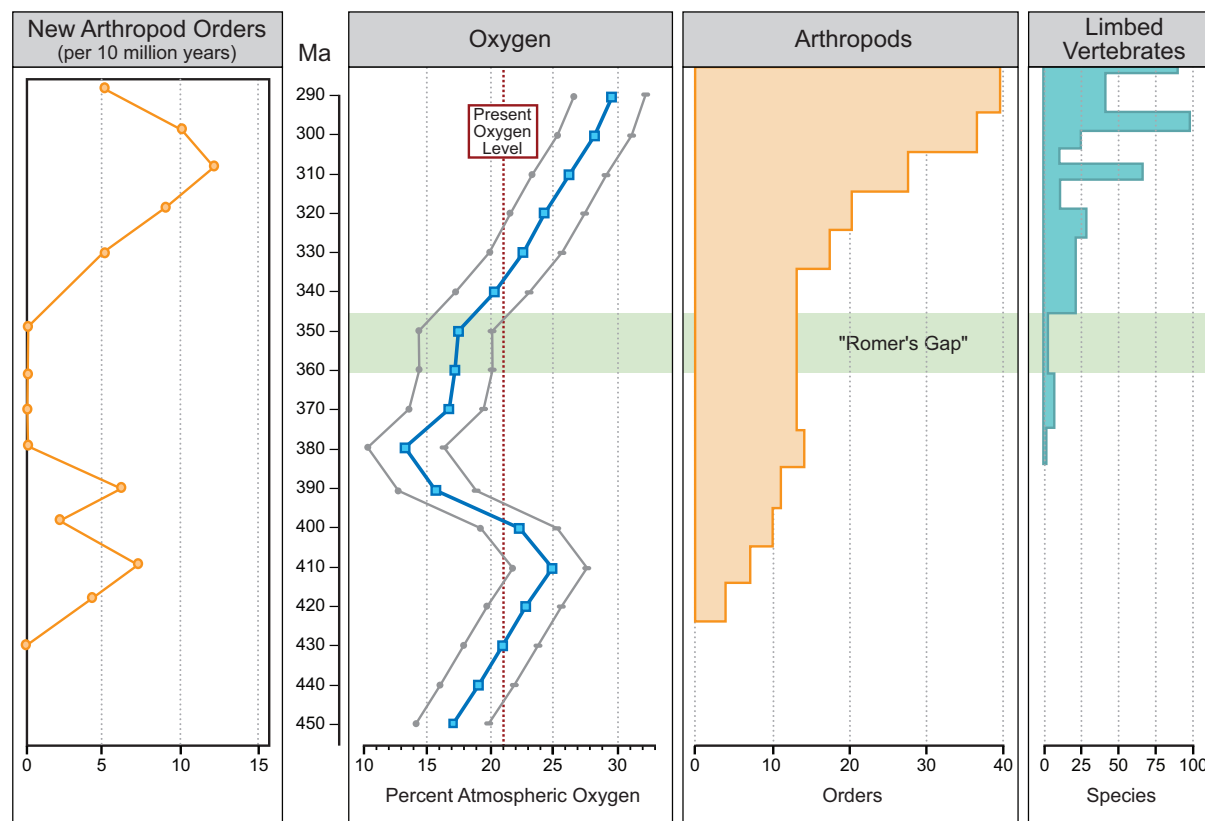
The authors declare no conflict of interest.

Abbreviations: MYBP, million years before present; My, million years.

<sup>†</sup>To whom correspondence may be addressed. E-mail: argo@u.washington.edu or robert.berner@yale.edu.

© 2006 by The National Academy of Sciences of the USA





**Fig. 2.** Ordinal-level diversity data for arthropods from Fig. 1, shown in 10-My bins, plotted against atmospheric  $O_2$  levels as computed with the GEOCARBSULF model and  $\pm 3\%$  error margins. Over the study interval  $O_2$  levels rise significantly above 21% (present level), then subside to  $<15\%$ , before a subsequent and sustained increase. The first event of Phase 1 land colonization by arthropods apparently is tied to rising atmospheric  $O_2$  with a slight time lag. Although both arthropod and limbed vertebrate clades survive the low- $O_2$  interval, they do so at low standing diversity, are composed of long-lived taxa, and are significantly supplemented by the emergence of minimally terrestrialized vertebrate clades in the second event of Phase 1 (from Fig. 1). Most revealing is that no new arthropod and very few stegocephalian taxa originate during the low- $O_2$  interval. A more dramatic Phase 2 of land colonization is linked to a second, more elevated rise in atmospheric  $O_2$ . Data are plotted as midpoints within 10-My bins.

brate taxa (Fig. 2) indicates that an increase in origination rate of new arthropod orders lagged  $\approx 10$  My behind a significant rise in maximal  $O_2$  levels ( $>20\%$ ) during  $\approx 435$ –400 MYBP. No terrestrialization of arthropods occurred before  $O_2$  levels reaching 20%, slightly less than the present level. The subsequent drop in  $O_2$  was followed by extinction of major arthropod clades, with all survivors belonging to long-lived lineages. No new clades appeared during the  $O_2$  minimum, the interval that largely coincides with Romer's Gap. This interval of 360–345 MYBP was preceded by the significant Frasnian to Fammenian (Late Devonian) mass extinction (375 MYBP), long interpreted to have been accompanied by (or perhaps caused by) periods of oceanic anoxia (14). These  $O_2$  data indicate that this interval of time also showed significantly lower levels of atmospheric  $O_2$  than occur today or was present earlier. Further evidence of these lower levels is shown by independent calculations based on rock abundance (15). Subsequently, diversification of terrestrial arthropods and vertebrates, also reflected in the appearance of new taxa, became associated with an increase in  $O_2$  commencing  $\approx 380$  MYBP. This  $O_2$  increase exceeded the present level of 21% at  $\approx 335$  MYBP and reached a subsequent peak of diversity, which coincided with maximum  $O_2$  levels often associated with arthropod gigantism (16).

### Discussion

The earliest macroscopic bryophyte-like and tracheophyte plants are assignable to taxa found from a relatively constrained Late Silurian to Early Devonian interval centered

from 425 to 400 MYBP, although the diversification of more crownward vascular plant lineages continued into the mid-Devonian to  $\approx 370$  MYBP (17, 18). Arthropod herbivores of these tracheophyte producers (19) as well as their trophically superjacent consumers consisted of three major arthropod clades that originated approximately at the same time and forever structured terrestrial ecosystems (2). These clades are myriapods, arachnids, and hexapods, although fungi also contributed a major role by providing intimate saprobic associations with both plants and arthropods (13, 20). Among initially radiating myriapods were diverse centipeded, millipeded, and arthropleurid clades, some of uncertain affinities (21, 22). Arachnid clades prominently included aerially respiring scorpions, trigonotarbids, pseudoscorpions, two mite lineages, and the earliest spiders (23), representing a broad spectrum of high-ranked taxa. By contrast, there is minimal evidence for a hexapod radiation, consisting of only collembolans and bristle-tails (2), albeit there is indirect evidence that perhaps winged insects were present (24). Based on Late Silurian to Middle Devonian fossil occurrences and cladistic sister-group relationships with extant taxa, these four major groups of organisms, tracheophyte plants, myriapods, arachnids, and hexapods, indicate the early establishment of major body plans assignable to terrestrial taxa and thus an early arthropod event (425–385 MYBP) within Phase 1 of land colonization by macroscopic but relatively small-sized animals. Currently, there is minimal evidence for a robust pattern of early diversification for hexapods. Ecological data also is supportive



evolution providing a vastly increased rate of organic matter burial in the form of biologically resistant lignin (35). Increased organic burial, reflecting augmented net photosynthesis (photosynthesis minus respiration), caused an increase in atmospheric O<sub>2</sub> during the mid-to-late Paleozoic (36). Recently, new carbon isotope data has become available (34), results of which have allowed refinements of previous model findings, especially for the early Paleozoic through Mesozoic interval. Most crucially for the work reported here, the

significant drop in oxygen found in an earlier study (15) has been reconfirmed.

We thank D. Ehlert and F. Marsh for drafting the figures and M. Carrano for commentary. This work was supported by the National Aeronautics and Space Administration (NASA) Astrobiology Institute (P.W.) and the Department of Energy (R.A.B.). This article is contribution 153 of the Evolution of Terrestrial Ecosystems Consortium at the National Museum of Natural History, Washington, DC.

1. Little C (1990) *The Terrestrial Invasion* (Cambridge Univ Press, Cambridge, UK).
2. Labandeira CC (2005) *Trends Ecol Evol* 20:253–262.
3. Clement G, Ahlberg PE, Blicek A, Blom H, Clack JA, Poty E, Thorez J, Janvier P (2004) *Nature* 427:412–413.
4. Clack JA, Ahlberg PE (2004) in *Recent Advances in the Origin and Early Radiation of Vertebrates*, eds Arratia G, Wilson MVH, Cloutier R (Friedrich Pfeil, Munich), pp 309–320.
5. Shubin NH, Daeschler EB, Coates MI (2004) *Science* 304:90–93.
6. Coates, M.I. Jeffery JE, Ruta M (2002) *Evol Dev* 4:390–401.
7. Clack JA (2002) *Gaining Ground: The Origin and Evolution of Tetrapods* (Indiana Univ Press, Bloomington, IN).
8. Coates MI, Clack JA (1991) *Nature* 352:234–236.
9. Clack JA (2002) *Nature* 418:72–76.
10. Romer AS (1966) *Vertebrate Paleontology* (Univ of Chicago Press, Chicago), 3rd Ed.
11. Coates MI, Clack JA (1995) *Bull Mus Nat Hist Nat* 17:373–388.
12. Laurin M, Giron dot M, de Ricqlès A (2000) *Trends Ecol Evol* 15:118–123.
13. Shear WA, Kukalová-Peck J (1990) *Can J Zool* 68:1807–1834.
14. Hallam A, Wignall P (1997) *Mass Extinctions and their Aftermath* (Oxford Univ Press, Oxford).
15. Berner RA, Canfield D (1989) *Am J Sci* 289:333–361.
16. Graham JB, Dudley R, Aguilar NM, Gans C (1995) *Nature* 375:117–120.
17. Kenrick P, Crane PR (1997) *The Origin and Early Diversification of Land Plants: A Cladistic Study* (Smithsonian Inst Press, Washington, DC).
18. Pryer KM, Schneider H, Magallón S (2004) in *Assembling the Tree of Life*, eds Cracraft J, Donoghue M (Oxford Univ Press, New York), pp 138–153.
19. Labandeira CC (1998) *Annu Rev Earth Planet Sci* 26:329–377.
20. Taylor TN, Klavins SD, Krings M, Taylor EL, Kerp H, Hass H (2004) *Trans R Soc Edinburgh Earth Sci* 94:457–473.
21. Labandeira CC (1999) in *Encyclopedia of Paleontology*, ed Singer R (Fitzroy Dearborn, Chicago), pp 767–775.
22. Wilson HM (2006) *J Paleontol* 80:638–649.
23. Selden PA, Dunlop JA (1998) in *Arthropod Fossils and Phylogeny*, ed Edgecombe G (Columbia Univ Press, New York), pp 303–331.
24. Engel MS, Grimaldi DA (2004) *Nature* 427:626–630.
25. Labandeira C (2006) *Geol Acta* 4:409–438.
26. Hilton J, Bateman RM (2006) *J Torr Bot Soc* 133:119–168.
27. Selden PA, Jeram AJ (1989) *Trans R Soc Edinburgh Earth Sci* 80:303–310.
28. Scholtz G, Kamenz C (2006) *Zoology* 109:2–13.
29. Falkowski PG, Katz ME, Knoll AH, Quigg A, Raven JA, Schofield O, Taylor FJR (2005) *Science* 305:354–360.
30. Ward PD (2006) *Out of Thin Air: Dinosaurs, Birds, and Earth's Ancient Atmosphere* (Joseph Henry, Washington, DC).
31. Labandeira C (1994) *Milwaukee Pub Mus Contr Biol Geol* 88:1–71.
32. Garrels RM, Lerman A (1984) *Am J Sci* 284:989–1007.
33. Berner RA, Petsch ST, Lake JA, Beerling DJ, Popp BN, Lane RS, Laws EA, Westley MB, Cassar N, Woodward FI, Quick WP (2000) *Science* 287:1630–1633.
34. Berner RA (2006) *Geochim Cosmochim Acta*, in press.
35. Robinson J (1990) *Geology* 15:607–610.
36. Berner RA (2004) *The Phanerozoic Carbon Cycle: CO<sub>2</sub> and O<sub>2</sub>* (Oxford Univ Press, Oxford).
37. Gradstein F, Ogg J, Smith A (2004) *A Geologic Time Scale 2004* (Cambridge Univ Press, Cambridge, UK).