Reports
tant role in locomotor propulsion than the forelimbs, which were probably important in food manipulation. Because of this, the body mass estimation based on the femur is more reliable. P. pattersoni probably weighed ~700 kg. With Phoberomys, the size range of the order is increased and Rodentia becomes one of the mammalian orders with the widest size variation, second only to the Diprotodontia (kangaroos, koalas, wombats, and possums) (fig. S1).

The fossil record of Caviomorpha is extensive, with 140 fossil genera recognized in a recent review (8), but no form competes with Phoberomys in terms of size. Artigasia magna from the upper Pliocene of Uruguay is reported to be gigantic, but its lower teeth are only ~60% of the size of those of P. pattersoni (19). Artigasia, like most fossil rodents, is known based only on dental and mandibular parts.

The paleoenvironment in which P. pattersoni was found and the associated fauna indicate that this rodent was either semi-aquatic or foraged in or near water, as capybaras do. P. pattersoni had a deep and massive horizontal ramus of the mandible, correlated with a high degree of hypsodonty. Phoberomys clearly had an abrasive diet, perhaps consisting of seagrasses. Potential predators could have been the many crocodiles reported from Urumaco, including some of the largest forms that ever existed, such as Purussaurus spp. Contemporary included Stupendemys geographicus, the world’s largest turtle (20).

References and Notes
cene Fauna of La Venta, Colombia (Smithsonian Institution, Washington, DC, 1997).
4. Léxico Estratigráfico de Venezuela (Ministerio de Energía y Minas, Boletín de Geología, Caracas, ed. 3, 1997).
8. M. C. McKenna, S. K. Bell, Classification of Mammals Above the Species Level (Columbia Univ. Press, New York, 1997).
16. Predictive equations for body size (15): log W = \[ a + \frac{b}{(log AF)} \] where W is body mass (in kilograms), log a is intercept, b is slope, and AF is the antero-
posterior diameter of the bone examined. Anteroposteri-
oraxial femur diameter (APF): log W = \[ \frac{1.678 + 2.518}{(1.80618)} \] W = 741.1; anteroposteri-
oraxial distal humerus diameter (APH): log W = \[ \frac{1.467 + 2.484}{(1.6532)} \] W = 436.1 kg.
18. The humerus/femur length ratio (H/F) and the (humerus + radius)/femur + ibia length ratio [H + R]/[F + T] in P. pattersoni (0.76 and 0.78, respectively) are average compared with those of other caviomorphs. For a sample of 17 extant caviomorphs, the mean values ± SD were H/F = 0.80 ± 0.08 and [H + R]/[F + T] = 0.74 ± 0.09. In the sample, there are no marked trends associated with growth or phylogeny (21). On the other hand, the ratios between femur versus humerus cross-
sectional diameters (APR/APH) (15) show that the hind-
limbs of P. pattersoni are robust. APR/APH is 1.42, whereas the average ± SD for a sample of 19 cavi-
omorph species (21) is 1.27 ± 0.18. Robust hindlimbs in comparison to forelimbs characterize also the dace composed of Dinomys, Chinchilla, and Lagostomus (mean ± SD = 1.40 ± 0.26), the closest relatives to Phoberomys among extant caviomorphs.
21. M. R. Sánchez-Villagra, O. Aguilera, I. Horovitz, un-
published data.
24. We added Lagostomus to the tree to increase the relevant sampling in our scaffold analysis. All rel-
vant treatments of caviomorph taxonomy and phylogeny place Lagostomus together with Chin-
chilla (22).
26. We thank J. Bocquentin, A. Ranci, A. Rincon, J. Reyes, D. Rodrigues da Aguilera, and R. Sánchez for help with fieldwork; J. Reyes and E. Weston for laboratory work; E. Weston and three anonymous reviewers for com-
ments on the manuscript; O. Aguilera Jr. for assist-
ance with digital imaging; S. Melendrez for recon-
struction of the skeleton of Phoberomys in Fig. 2; D. Mörke (Stuttgart) and E. Weber (Tübingen) for ac-
tess to collections; and J. Bocquentin and A. Ranci for preliminary work on the identification of the giant rodent. Work in Venezuela by M.R.S.-V. was partially supported by the National Geographic Society and the University of Tübingen. The Smithsonian Tropical Research Institute and the Universidad Nacional Ex-
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search Associate of the Smithsonian Tropical Re-
search Institute.

Supporting Online Material
www.sciencemag.org/cgi/content/full/301/5640/1708/ DC1 SOM Text Fig. 51 Tables S1 to S3 References
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Amazonia 1492: Pristine Forest or Cultural Parkland?

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Archaeological evidence of the Amazonian landscape in the Upper Xingu region of Brazil reveals unexpectedly complex regional settlement patterns and large-scale transformations of local landscapes over the past millennia. Mapping and excavation of archaeological structures document pronounced human-induced alteration of the forest cover, particularly in relation to large, dense late-prehistoric settlements (circa 1200 to 1600 A.D.). The findings contribute to debates on human carrying capacity, population size and settlement patterns, anthropogenic impacts on the environment, and the importance of indigenous knowledge, as well as contributing to the pride of place of the native peoples in this part of the Amazon.

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Was the Amazon a natural forest in 1492, sparsely populated and essentially pristine, as has been traditionally thought? Or, instead, were parts of it densely settled and better viewed as cultural forests, including large agricultural areas, open parklands, and working forests associated with large, regional polities (1–3). Despite growing popularity for the latter view (4–6), entrenched debates re-

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under indigenous resource management [Parque Indigena do Xingu (PIX)]. It remains little affected by 20th century mechanized development (Fig. 1). The Upper Xingu is a long-standing case study of indigenous Amazonian agriculture and ecology (9, 10) and one of the few places where contemporary observations of indigenous agriculture, land use, and settlement pattern can be systematically linked with archaeological and oral historical evidence (11). Long-term in situ cultural development of Xinguano peoples over more than 1000 years (12) is clearly documented by continuity in (i) utilitarian ceramics used to process and cook staple foods (13); (ii) settlement placement (at forest/wetland transitions) and local land use, marked by substantial forest and wetland alterations; and (iii) settlement form, notably circular plazas with radial roads (14) (movie S1).

In the Kuikuro study area (Fig. 2) (15), 19 major pre-Columbian settlements have been identified, generally separated by 3 to 5 km and linked by a system of broad, straight roads (16). Recognition and mapping of major earthworks at these sites reveal their articulation in a remarkably elaborate regional plan (14). The earthworks include (i) excavated ditches in and around ancient settlements (up to 2.5 km long and 5 m deep); (ii) linear mounds or “curbs” positioned at the margins of major roads and circular plazas (averaging about 0.5 to 1.0 m in height); and (iii) a variety of wetland features, such as bridges, artificial river obstructions and ponds, raised causeways, canals, and other structures, many of which are still in use today. Similar constructed features (such as settlements, roads, weirs, and ponds) are known from culturally related peoples (principally Arawak speakers) across the southern Amazonian periphery (17–19) [supporting online material (SOM) text].

The integrated settlement configuration was in place by c. 1250 to 1400 A.D., based on radiocarbon dates from stratified deposits at X6, X11, and X13 (Table 1) (14, 20). Major curbed roads (10 to 50 m wide) articulate with plazas, ditches, and partition space within villages and across the broader landscape, notably linking settlements into “galactic” clusters across the region (21). The Ipatse cluster includes four major residential settlements (X6, X17, X18, and X22), linked to a fifth unfortified “hub” site (X13), with only limited residential occupation (Fig. 3A). Another cluster of sites, centered on X11, shows a similar pattern of a large (50 ha) fortified settlement connected to other smaller but still elaborate settlements. In the case of the Kuikikugu (X11) cluster, the largest residential center is the hub (Fig. 3B). The primary nodes of each cluster are also linked by roads to smaller plaza settlements (fig. S1). On the basis of artifact and dark-earth distributions, it has been estimated that large sites, such as X6 and X11, had 15 to 25 ha of residential space, medium sites (X17, X18, X22) had 5 to 10 ha, and small sites had 2 to 5 ha (14).

Thus, the actual residential area of a cluster like X6 or X11 was at least 40 to 80 ha in an area of about 400 km², with an estimated population of between 2500 and 5000 persons (or about 6 to 12.5 persons per km² in the study area).

Areas within each galactic cluster can be characterized as saturated anthropogenic landscapes, because virtually the entire area in and between major settlements, although not entirely cultural in origin, was carefully engineered and managed. Indeed, the road networks, oriented by the same system of cardinality that characterizes plaza spatial organization, partitioned the landscape into a gridlike or latticelike organization of nodes (plazas) and connecting thoroughfares, although patches and corridors of secondary and perhaps managed forests were likely common, as they are today. Mapped archaeological features correspond to patches of acutely modified secondary growth, distinctive from surrounding forest and easy to recognize in

Fig. 2. Kuikuro study area showing the distribution of major ditched plaza centers (stars in circles), major plaza centers (open circles), and small plaza and non-plaza villages (black dots).
Ditch the mid-ditch text).

Fieldwork in 2003 demonstrates that roads extend fully from X13 to X18, and continue on to X19, X20, and beyond along the north-south road, as well as across high ground to X17 and X22 (fig. S1); X11 roads also connect it to the four satellites. MTFX, Mato Grosso (the state), Formadores do Xingu (the archaeological region). The number refers to the site number.

Table 1. Radiocarbon dates from Nokugu (X6) and other sites in the Kuikuro study area, southern PIX. Beta 176135 to Beta 176144 are reported here for the first time. Calibrated age ranges for samples dated in 2003 (numbered 176135 and up) were reported by Beta-Analytic laboratory; previous (1994) dates were calibrated using CALIB 4.0 (29). ET, excavation trench of 1.0 by 10.0 m or more; EU, excavation unit of 1.0 m²; S, southern side of plaza or site; N, northern side; Ditch 1, outermost; Ditch 2, middle; Ditch 3, innermost ditch in all sites.

<table>
<thead>
<tr>
<th>Lab no.</th>
<th>Site/unit</th>
<th>Conventional radiocarbon</th>
<th>2σ-calibrated age range</th>
<th>Provenience</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Historical Xinguano (1700 A.D.–present)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta 176142</td>
<td>X6/ET2</td>
<td>20 ± 50</td>
<td>modern*</td>
<td>Ditch 3 (S), upper ditch infill</td>
</tr>
<tr>
<td>Beta 176143</td>
<td>X6/ET2</td>
<td>670 ± 60</td>
<td>1260–1410 A.D.</td>
<td>Ditch 3 (N), basal fill</td>
</tr>
<tr>
<td>Beta 176144</td>
<td>X6/ET1</td>
<td>440 ± 60</td>
<td>1260–1480 A.D.</td>
<td>Small plaza, subcurb intact</td>
</tr>
<tr>
<td>Beta 176145</td>
<td>X6/ET1</td>
<td>690 ± 60</td>
<td>1260–1300 A.D.</td>
<td>Central plaza, subcurb intact</td>
</tr>
<tr>
<td>Beta 176146</td>
<td>X6/ET1</td>
<td>700 ± 70</td>
<td>1230–1410 A.D.</td>
<td>Ditch 2 (S), sub-berm intact</td>
</tr>
<tr>
<td>Beta 176147</td>
<td>X6/ET2</td>
<td>900 ± 60</td>
<td>1000–1250 A.D.</td>
<td>Central plaza, subcurb intact</td>
</tr>
<tr>
<td>Beta 176148</td>
<td>X6/ET2</td>
<td>910 ± 80</td>
<td>1040–1250 A.D.</td>
<td>Central plaza, subcurb base intact</td>
</tr>
<tr>
<td>Beta 176149</td>
<td>X6/ET2</td>
<td>1000 ± 70</td>
<td>950–1210 A.D.</td>
<td>Ditch 2 (S), sub-berm, base intact</td>
</tr>
<tr>
<td>Beta 176150</td>
<td>X6/ET3</td>
<td>1260 ± 60</td>
<td>980–1300 A.D.</td>
<td>Central plaza, subcurb base intact</td>
</tr>
<tr>
<td><strong>Terminal “galactic” period (1400–1700 A.D.)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta 176151†</td>
<td>X6/ET2</td>
<td>590 ± 60</td>
<td>1300–1420 A.D.</td>
<td>Ditch 3 (N), basal fill</td>
</tr>
<tr>
<td>Beta 176152†</td>
<td>X6/ET2</td>
<td>670 ± 60</td>
<td>1260–1410 A.D.</td>
<td>Ditch 3 (N), basal fill</td>
</tr>
<tr>
<td>Beta 176153†</td>
<td>X6/ET1</td>
<td>440 ± 60</td>
<td>1260–1480 A.D.</td>
<td>Small plaza, subcurb intact</td>
</tr>
<tr>
<td>Beta 176154†</td>
<td>X6/ET1</td>
<td>690 ± 60</td>
<td>1260–1300 A.D.</td>
<td>Central plaza, subcurb intact</td>
</tr>
<tr>
<td>Beta 176155†</td>
<td>X6/ET1</td>
<td>700 ± 70</td>
<td>1230–1410 A.D.</td>
<td>Ditch 2 (S), sub-berm intact</td>
</tr>
<tr>
<td>Beta 176156†</td>
<td>X6/ET2</td>
<td>710 ± 50</td>
<td>1270–1300 A.D.</td>
<td>Ditch 1 (S), basal fill</td>
</tr>
<tr>
<td><strong>Late developmental (900–1250 A.D.)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta 176157†</td>
<td>X6/ET2</td>
<td>900 ± 60</td>
<td>1000–1250 A.D.</td>
<td>North road, subcurb, basal intact</td>
</tr>
<tr>
<td>Beta 176158†</td>
<td>X6/ET2</td>
<td>910 ± 80</td>
<td>1040–1250 A.D.</td>
<td>Central plaza, subcurb base intact</td>
</tr>
<tr>
<td>Beta 176159†</td>
<td>X6/ET1</td>
<td>1000 ± 70</td>
<td>950–1210 A.D.</td>
<td>Ditch 2 (S), sub-berm, base intact</td>
</tr>
<tr>
<td>Beta 176160†</td>
<td>X6/ET3 1</td>
<td>1260 ± 60</td>
<td>980–1300 A.D.</td>
<td>Central plaza, subcurb base intact</td>
</tr>
<tr>
<td><strong>Initial Xinguano (pre-900 A.D.)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta 176161†</td>
<td>X6/ET2</td>
<td>1370 ± 60</td>
<td>640–690 A.D.</td>
<td>Mid-ditch 3 (N), mid-ditch</td>
</tr>
<tr>
<td>Beta 176162†</td>
<td>X6/ET10</td>
<td>2110 ± 40</td>
<td>190–60 B.C.</td>
<td>Ditch (N), basal fill</td>
</tr>
</tbody>
</table>

*Two additional modern dates, Beta 98978 and Beta 176144, are considered invalid. The former was redated with a sample slightly higher in profile (Beta 81301).†Beta 176139 is inversely with Beta 176143 and was redated by 177724. Beta 176138 also comes from stratified but mixed context of ditch infill, and both likely represent earlier materials that are mixed in ditch construction.

These patches or islands are identified in the indigenous knowledge systems, including diverse species whose distributions are generally restricted to anthrosols (dark earth)—called egepe by the Kuikuro—associated with ancient settlements (22–24) (SOM text). Some areas related to major pre-Columbian settlements, like X6, X11, and X13, have not returned to high forest after about 400 years of abandonment, although other areas (such as roads, hamlets, gardens, fields, and parklands) show a highly patchy forest regrowth typical of postabandonment (after 1600 to 1750) succession.

Recognition of the massive forest alterations associated with pre-Columbian occupations requires an understanding of local biodiversity in the context of the complex cultural history of the area. The composition of forest and wetland habitats reflects long-term cumulative changes, given that the settlement areas were occupied more or less continuously over many generations, as well as the large-scale alteration and management of local environments by dense late-prehistoric occupations (c. 1250 to 1650 A.D.). Present soil and biotic distributions, often isomorphic with the distribution of archaeological features, notably plazas, residential areas, roads, and roadside hamlets, are in large part the result of pre-Columbian land-management strategies. After c. 1600 to 1700, catastrophic
depopulation (25) led to the abandonment of these works and many settlements, resulting in extensive reforestation in many areas. The scale of the prehistoric settlements, including exterior constructions, such as roads, hamlets, wetland structures, and cultivation areas, suggests that agricultural and parkland landscapes, rather than high forest, characterized the broad landscapes around ancient villages, as is true in contemporary villages. Metal technology, however, has increased the speed at which forests can be converted into mosaic parklands of dispersed manioc gardens, sapé grass fields, piqui groves, and secondary forests (26) (Fig. 4).

The Upper Xingu is a unique Amazonian example of a tropical forest way of life that supported large, densely settled, and integrated regional populations over the past 1000 years. Local ecology reflects the dynamic interaction between the natural environment, the influence of fairly large, settled human populations, and the legacy of Euro-American colonialism over the past ~500 years. Evidence of large, well-engineered public works (such as plazas, roads, moats, and bridges) in and between pre-Columbian settlements suggests a highly elaborate built environment, rivaling that of many contemporary complex societies of the Americas and elsewhere (SOM text). To suggest that Xinguano lands were intensively managed and developed, c. 1492, however, does not imply that indigenous land-use strategies, based on patchy development within long rotational cycles, are comparable to modern nonindigenous clear-cutting strategies (27, 28). Xinguano cultivation and land management, indeed, provides a viable alternative. The present research emphasizes the critical importance of collaborative research strategies, including archaeological and ethnographic fieldwork, remote-sensed data analysis and geographic information systems, and most important, indigenous participation, to understand the complex interplay of ecological, historical, and political conditions in Amazonia before and after 1492.

References and Notes
12. Initial Xinguano occupations date sometime between 200 B.C. and 800 A.D., but the exact date is uncertain because the two earliest radiocarbon dates are from mixed deposits, and in one case (Beta-Analytic Laboratory number 176143) the dates are demonstrably out of sequence.
13. Manioc, fish, and piqui fruit constitute 90% or more of the diet (9).
14. Materials and methods are available as supporting material on Science Online.
15. The Xingu study area is about the same as the same as the Xingu (Carib-Xinguano) traditional territory. It is about 1000 km² and is located in an area of traditional Xinguano occupations that is 25,000 to 35,000 km².
16. Several additional large sites are known in the study area, on the basis of indigenous knowledge of dark-earth locations, and numerous smaller occupation sites are also known, including small road-side hamlets along the major roads.
20. Here, “galactic” describes the regional site clusters organized around a center or hub (X11 and X13), with several major residential sites connected to it.
22. Dark earth forms in compost areas, although widespread burning produces minor but extensive soil alterations.
30. Ethnoarchaeological research in the Upper Xingu by M.J.H., conducted in collaboration with the Museu Nacional (UFRJ), the Museu Goeldi, and the
Resurrecting the Ancestral Steroid Receptor: Ancient Origin of Estrogen Signaling

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Receptors for sex and adrenal steroid hormones are absent from fully sequenced invertebrate genomes and have not been recovered from other invertebrates. Here we report the isolation of an estrogen receptor ortholog from the mollusk *Aplysia californica* and the reconstruction, synthesis, and experimental characterization of functional domains of the ancestral protein from which all extant steroid receptors (SRs) evolved. Our findings indicate that SRs are extremely ancient and widespread, having diversified from a primordial gene before the origin of bilaterally symmetric animals, and that this ancient receptor had estrogen receptor–like functionality. This gene was lost in the lineage leading to arthropods and nematodes and became independent of hormone regulation in the *Aplysia* lineage.

Vertebrate genomes contain six evolutionarily related nuclear receptors for steroid hormones: two for estrogens (ERα and ERβ) and one each for androgens (AR), progestins (PR), glucocorticoids (GR), and mineralocorticoids (MR). These ligand-activated transcription factors mediate the actions of hormones that direct sexual differentiation, reproduction, behavior, immunity, and stress response (1). There are no orthologs of these genes in the insect *Drosophila melanogaster*, the nematode *Caenorhabditis elegans*, or the urochordate *Ciona intestinalis* (2, 3), and a polymerase chain reaction (PCR) screen (4) failed to identify any of these genes outside the vertebrates. The most closely related nuclear receptors are the estrogen-related receptors (ERRs), an ortholog of which is present in the fruit fly genome (2). Based on this gene distribution, steroid receptors (SRs) are thought to have evolved in the chordate lineage some 400 to 500 million years ago, due to a duplication of a more ancient ERR gene (4–6). Estrogens and other vertebrate-type steroids appear to be involved in the reproductive endocrinology of certain mollusks, however (7, 8). Further, arthropods and nematodes are relatively closely related within the Edyszoan clade of molting organisms (9), suggesting the possibility that the SR family may have been lost in the lineage leading to both phyla. A previous analysis of SR sequences indicated that the ancient progenitor of this protein class was most similar to extant ERs (10).

We used degenerate PCR and rapid amplification of cDNA ends to isolate an ER sequence (figs. S1 and S2) from a mollusk, the sea hare *Aplysia californica*. Using primers derived from vertebrate ERs, we amplified an ER-like cDNA sequence from both adult neural tissue and ovotestes of *A. californica* (11). The protein sequence of the *Aplysia* receptor’s DNA-binding domain (DBD) is highly similar to that of the vertebrate ERs but much less similar to those of other nuclear receptors, including the ERRs (Fig. 1A). Within the DBD, the P box, which mediates recognition of specific response elements by estrogen and other SRs (12), is identical only to that of the human ERs (Fig. 1B). The ligand-binding domain (LBD) of the *Aplysia* receptor is less conserved but is also most similar to that of the vertebrate ER. The *Aplysia* receptor’s AF-2 activation domain—a small region in the LBD that mediates ligand-regulated interactions with coactivators (13)—is nearly identical to that of the human ERs but not to those of the ERRs or other SRs (Fig. 1B).

The true test of orthology is phylogeny, so we analyzed the relations among 74 steroid and related receptors, including the *Aplysia* ER, using maximum parsimony (MP) and Bayesian Markov Chain Monte Carlo (BMC) techniques (11). Both methods (Fig. 2A) strongly indicate that the *Aplysia* sequence is an ortholog of the vertebrate ERs. The node indicating orthology with the vertebrate ERs is well supported, with a BMC posterior probability of 100%, a bootstrap proportion of 90%, and a decay index of 6. Although BMC probabilities can sometimes overestimate statistical confidence (14), a 90% bootstrap normally indicates confidence well over 95% (15). Further, the maximum likelihood of this phylogeny is >100,000 times greater than that of the best phylogeny in which the *Aplysia* receptor is placed outside the clade of SRs. As this phylogeny shows, the gene duplication that produced the first SR preceded the ancient divergence of deuterostomes (the superphylum that includes chordates and echinoderms) from protostomes [mollusks, arthropods, nematodes, anne-

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**Fig. 1.** The *Aplysia* ER protein sequence is most similar to that of human ERs. (A) Percent similarity of the *Aplysia* ER to steroid and related receptors of vertebrates and insects in the DNA- and ligand-binding domains. (B) Detail of sequences in the P box of the DBD, which mediates recognition of the core response element on DNA; in the AF-2 activation function of the ligand-binding domain, which is essential for ligand-activated transcription; and in the C-terminal extension (CTE) of the protein, with the length of the CTE in amino acids indicated. Dots show residues identical to those of *Aplysia* ER; an asterisk indicates the end of the coding sequence.