To examine the temporal profile of ChC production and their correlation to laminar deployment, we injected a single pulse of BrdU into pregnant Nkx2.1CreER;R26R females at successive days between E15 and P1 to label mitotic progenitors, each paired with a pulse of tamoxifen at E17 to label Nkx2.1CreER;R26R cells (Fig. 3A). We first quantified the fraction of L2 ChCs (identified by morphology) in MPCs that were also BrdU+. Although there were ChC production by E17, when MGE has morphologically disappeared and Nkx2.1 expression has appeared at VGZ, they further demonstrate that the identity of NKX2.1-progenitors in VGZ and their extended neurogenesis might have evolved, since rodents, to enrich and diversify cortical interneurons, including ChCs.

Studies in numerous systems (19) have demonstrated that the specification of neuronal identities early in development exerts strong influences in their subsequent positioning, connectivity, and function, but, to what extent this principle applies to the assembly of cortical networks has been unclear. Here, we discovered that young chandelier cells, once specified through their lineage and birth time in the VGZ, migrate with a stereotyped route and achieve distinct laminar patterns before inaugurating a subdomain of PyN AIS. Therefore, interneurons with a distinct identity are likely endowed with cell-intrinsic programs that contribute to their subsequent integration into their destined cortical networks. Deficiencies in ChCs have been implicated in brain disorders, including schizophrenia (20). Genetic targeting of ChCs establishes an entry point that integrates studies of fate specification, laminar deployment, connectivity, and network dynamics in the context of cortical circuit assembly and function. This may provide a probe to circuit pathogenesis in models of neuropsychiatric disorders.

References and Notes

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Materials and Methods
Fig. S1 to S8 Tables S1 and S2 References (21, 22) Movie S1
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An Update of Wallace’s Zoogeographic Regions of the World

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Zoogeographic Regions of the World

Modern attempts to produce biogeographic maps focus on the distribution of species, and the maps are typically drawn without phylogenetic considerations. Here, we generate a global map of zoogeographic regions by combining data on the distributions and phylogenetic relationships of 21,037 species of amphibians, birds, and mammals. We identify 20 distinct zoogeographic regions, which are grouped into 11 larger realms. We document the lack of support for several regions previously defined based on distributional data and show that spatial turnover in the phylogenetic composition of vertebrate assemblages is higher in the Southern than in the Northern Hemisphere. We further show that the integration of phylogenetic information provides valuable insight on historical relationships among regions, permitting the identification of evolutionary unique regions of the world.

Biogeographic and bioclimatic regions are the fundamental units of comparison in many broad-scale ecological and evolutionary studies (1, 2) and provide an essential tool for conservation planning (3, 4). In 1876, Alfred Russel Wallace published the first map of global terrestrial zoogeographic regions (5), which later became the cornerstone of modern biogeography
(3). Using existing knowledge of his time (6), mostly on the distributions and taxonomic relationships of broadly defined vertebrate families, Wallace divided the world into six terrestrial zoogeographic units largely delineated by what we now know as the continental plates. Despite relying on limited information and lacking a statistical basis, Wallace’s original map is still in use today.

Wallace’s original zoogeographic regionalization scheme considered ancestral relationships among species, but subsequent schemes generally used data only on the contemporary distributions of species without explicitly considering phylogenetic relationships (7–9). Phylogenetic trees contain essential information on the evolutionary relationships of species and have become increasingly available in recent decades, permitting the delineation of biogeographic regions as originally envisioned by Wallace.

Fig. 1. Map of the terrestrial zoogeographic realms and regions of the world. Zoogeographic realms and regions are the product of analytical clustering of phylogenetic turnover of assemblages of species, including 21,037 species of amphibians, nonpelagic birds, and nonmarine mammals worldwide. Dashed lines delineate the 20 zoogeographic regions identified in this study. Thick lines group these regions into 11 broad-scale realms, which are named. Color differences depict the amount of phylogenetic turnover among realms. (For more details on relationships among realms, see the dendrogram and NMDS plot in fig. S1.) Dotted regions have no species records, and Antarctica is not included in the analyses.

Wallace’s zoogeographic regions are the product of analytical clustering of phylogenetic turnover of assemblages of species, including 21,037 species of amphibians, nonpelagic birds, and nonmarine mammals worldwide. Dashed lines delineate the 20 zoogeographic regions identified in this study. Thick lines group these regions into 11 broad-scale realms, which are named. Color differences depict the amount of phylogenetic turnover among realms. (For more details on relationships among realms, see the dendrogram and NMDS plot in fig. S1.) Dotted regions have no species records, and Antarctica is not included in the analyses.
Strait between Borneo and Sulawesi, now known as “Wallace’s Line” (15), was a major barrier to dispersal that greatly inhibited exchanges between the Australian and Asian land masses. Much debate subsequently arose regarding the precise location of the principal faunal divide between Wallace’s Oriental and Australian realms (15) (see fig. S3 for an illustration of Wallace’s original line). Our combined taxa analyses lend the strongest support to the hypothesis of Weber (16), who positioned this boundary east of Sulawesi, corresponding to the zoogeographic boundary separating our Oriental and Oceanian realms (Fig. 1 and fig. S1). However, our taxon-specific geographic delineation for birds is more consistent with Wallace’s line than Weber’s line (Fig. 3A and figs. S3 and S4A).

The delineation of and relationships among our zoogeographic regions differ among taxa (Fig. 3 and fig. S4), and we find more regions for mammals (n = 34 regions) than for amphibians or birds (both n = 19 regions). A comparison of pb matrices across the three vertebrate taxa reveals that amphibian assemblages located in the northeastern Arctico-Siberian, southern African, and Madagascan regions are more phylogenetically distinct than those of birds or mammals for the same regions (fig. S5). Moreover, the Australian region harbors more phylogenetically distinct assemblages of amphibians and mammals relative to birds (fig. S5). Using a partial Mantel test [see (13) for details on this analysis], which accounts for geographic distances among species assemblages (17), we find that global pb values for birds and mammals are more strongly correlated (r = 0.68, P < 0.001) than for amphibians and birds (r = 0.39, P < 0.001) or amphibians and mammals (r = 0.43, P < 0.001). These results might partly reflect a major episode of diversification early in the evolutionary history of amphibians (18). Alternatively, differences in spatial patterns of phylogenetic turnover among vertebrate classes might result from lower dispersal ability (19) and greater sensitivity of amphibians to environmental conditions (20). Interestingly, previous comparative studies documented similar incongruence in the diversity and distribution of amphibians relative to that of birds and mammals (21, 22).

The contrast between our zoogeographic regions with regions based only on distributional data (Fig. 4) demonstrates the consequences of incorporating phylogenetic information in the delineation of zoogeographic units. Relative to expectations based on turnover of species, spatial turnover in the phylogenetic composition of assemblages of species is generally low in the...
Northern Hemisphere, whereas the opposite is true in the Southern Hemisphere (Fig. 4A). In particular, amphibians exhibit low spatial turnover in phylogenetic composition relative to their turnover in the composition of species between the North American and Eurasian regions (Fig. 4B; also compare fig. S4A with fig. S6A). Higher phylogenetic uniqueness in the Southern than in the Northern Hemisphere is consistent with long-term isolation having left a pervasive signature on species assemblages, where oceanic barriers have limited dispersal between continents (23, 24).

In the Northern Hemisphere, the newly defined boundaries of the Palearctic realm might reflect the continuous presence of nonglaciated tundra in eastern Siberia and Beringia (25), whereas the subtle differences in the phylogenetic composition of assemblages over the Northern Hemisphere as a whole might be a consequence of a high degree of connectivity and range dynamics. Low rates of extinctions resulting from greater climatic stability in the Southern Hemisphere could also have contributed to this pattern by allowing species that belong to ancient clades to persist through time (26, 27).

Our maps of zoogeographic realms and regions provide a broad overview of the distribution of the world’s amphibians, birds, and nonmarine mammals, allowing the identification of geographic areas harboring distinct evolutionary histories [see (28) for links to downloadable maps of zoogeographic realms and regions for projection in GIS (geographic information systems) mapping software and Google Earth]. These maps reflect major advances made in recent decades regarding our knowledge of the distribution and phylogeny of vertebrates and can be used to elucidate the forces and historical events responsible for the formation of the biogeographic realms and regions we recognize today. Our delineation of the zoogeographic realms and regions of the world, and especially that of the realms, appears robust to the type and quality of distributional and phylogenetic data used [see (13) for details]. Inclusion of additional phylogenetic information on branch length or improved resolution of the phylogenetic trees has the potential to facilitate a finer delineation of regions within our realms. The inclusion of data (when they become available) on reptiles, invertebrates, and/or plants may also affect the boundaries of our realms and regions and the relationships among them. Nevertheless, the maps presented here delineate robust zoogeographic units for vertebrates that can be scaled within specific continents and/or taxonomic clades. Due to these qualities, our analytical approach and zoogeographic maps provide a baseline for a wide variety of comparative ecological, biogeographic, evolutionary, and conservation-based studies (3, 22, 29).

References and Notes
12. A. R. Wallace and his contemporary W. L. Sclater used the terms “region” to denote six main zoogeographical units at a global scale and “subregion” to denote finer scale subdivisions. Wallace’s and Sclater’s regions and subregions are roughly equivalent to the realms and regions proposed here. The work of Sclater was published in The Geographical Journal (1894–1897).
13. Materials and methods are available as supplementary materials on Science Online.
17. N. Mantel, Cancer Res. 27, 209 (1967).
28. Downloadable maps of zoogeographic realms and regions for visualization in GIS and Google Earth can be found at http://macroecology.ku.dk/resources/wallace.

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Crocodile Head Scales Are Not Developmental Units But Emerge from Physical Cracking

Michel C. Milinkovitch, Liana Manukyan, Adrien Debry, Nicolas Di-Poi, Samuel Martin, Daljit Singh, Dominique Lambert, Matthias Zwicker

Various lineages of amniotes display keratinized skin appendages (feathers, hairs, and scales) that differentiate in the embryo from genetically controlled developmental units whose spatial organization is patterned by reaction-diffusion mechanisms (RDMs). We show that, contrary to skin appendages in other amniotes (as well as body scales in crocodiles), face and jaws scales of crocodiles are random polygonal domains of highly keratinized skin, rather than genetically controlled elements, and emerge from a physical self-organizing stochastic process distinct from RDMs: cracking of the developing skin in a stress field. We suggest that the rapid growth of the crocodile embryonic facial and jaw skeleton, combined with the development of a very keratinized skin, generates the mechanical stress that causes cracking.

Amniotes exhibit a keratinized epidermis preventing water loss and skin appendages that play major roles in thermoregulation, photoprotection, camouflage, behavioral display, and defense against predators. Whereas mammals and birds evolved hairs and feathers, respectively, reptiles developed various types of scales. Although their developmental processes share some signaling pathways, it is unclear whether mammalian hairs, avian feathers and feet scales, and reptilian scales are homologous or if some of them evolved convergently (1). In birds and mammals, a reaction-diffusion mechanism (RDM) (2) generates a spatial pattern of placodes that develop and differentiate into follicular organs with a dermal papilla and cycling growth of an elongated keratinized epidermal structure (hairs or feathers) (3). However, scales in reptiles do not form true follicles and might not develop from placodes (4). Instead, reptilian scales originate in the embryo from regular dermoepidermal elevations (1). Whereas the regular spatial organization of scales on the largest portion of the reptilian body is determined by a RDM, additional positional cues are likely involved in the development of the scale plates present on the head of many snakes and lizards. These head scales form a predictable symmetrical pattern (Fig. 1A) and provide mechanical protection.

The face and jaws of crocodilians are covered by polygonal scales (hereafter called “head scales”) that are strictly adjoining and nonoverlapping, but these polygons are irregular and their spatial distribution seems largely random (Fig. 1, B and C). Using high-resolution three-dimensional (3D) geometry and texture reconstructions (5–7),

**Fig. 1.** Spatial distribution of head scales. (A) Head scales in most snakes (here, a corn snake) are polygons (two upper panels) with stereotyped spatial distribution (two lower panels): left (yellow) and right (red) scale edges overlap when reflected across the sagittal plane (blue). (B) Polyonal head scales in crocodiles have a largely random spatial distribution without symmetrical correspondence between left and right. (C) Head scales from different individuals have different distributions of scales’ sizes and localizations (blue and red edges from top and bottom crocodiles, respectively).
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