for estimating species trees from genome-scale concatenated sequence alignments (SM4) (55–57). We also developed a statistical binning approach that improves multispecies coalescent analyses for handling gene trees with low phylogenetic signal to infer a species tree (SM5) (58). These computationally intensive analyses were conducted on more than 9 supercomputer centers and required the equivalent of >400 years of computing using a single processor (SM3 and SM4).

From these efforts, we identified a high-quality orthologous gene set across avian species, consisting of exons from 8251 syntenic protein-coding genes (~40% of the proteome), introns from 2516 of these genes, and a nonoverlapping set of 3769 ultraconserved elements (UCEs) with ~1000 bp of flanking sequences. This total evidence nucleotide data set comprised ~41.8 million bp (table S3 and SM4), representing ~3.5% of an average avian genome.

Total evidence nucleotide tree

The total evidence nucleotide alignment partitioned by data type (introns, UCEs, and first and second exon codon positions; third positions excluded as described later) analyzed with ExaML under the GTR+GAMMA model of sequence evolution (SM4) resulted in a highly resolved total evidence nucleotide tree (TENT) (Fig. 1 and fig. S1). The three recognized major groupings within extant birds—Palaeognathae, Galloanseres, and Neoaves (the latter two united in the infraclass Neognathae)—were recovered with full (100%) bootstrap support (BS). The tree revealed the first divergence within extant Neoaves, resulting in two fully supported, reciprocally monophyletic sister clades that we named Passerea (after its most speciose group Passeriformes) and Columbea (after its most speciose group Columbiformes) (Fig. 1; see SM6 for rationale of clade names).

Within Passerea, the TENT strongly confirmed the monophyly of two large closely related clades that we refer to as core landbirds (Telluraves) and core waterbirds (Aequornithia) (8,16,17,27,36,59);