Figures and figure supplements

Between-species variation in neocortical sulcal anatomy of the carnivoran brain

Magdalena Boch *et al.*

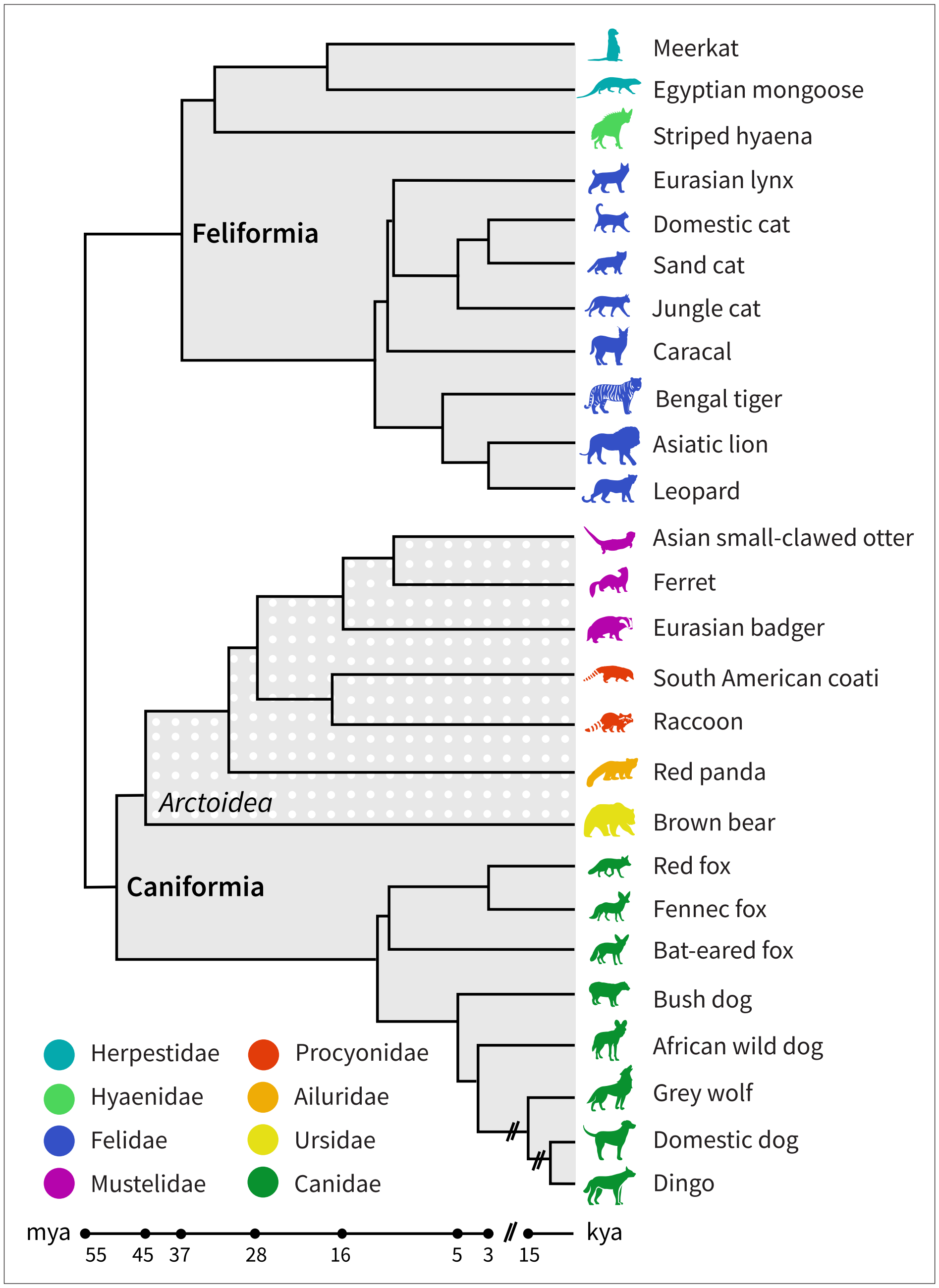

Figure 1. Phylogeny of carnivoran sample. The sample consists of species from both carnivoran sub-orders, Caniformia and Feliformia and includes members of eight different families (see also ***Table 1*** in **Materials and methods** for a detailed sample description). The sub-order Caniformia includes Canidae and five Arctoidea families. All animals are terrestrial, except for the semi-aquatic Asian small-clawed otter. Phylogenetic relationships were derived from ***Field et al., 2022***; ***Freedman et al., 2014***; ***Kumar et al., 2017***. k/mya, thousand/million years ago.

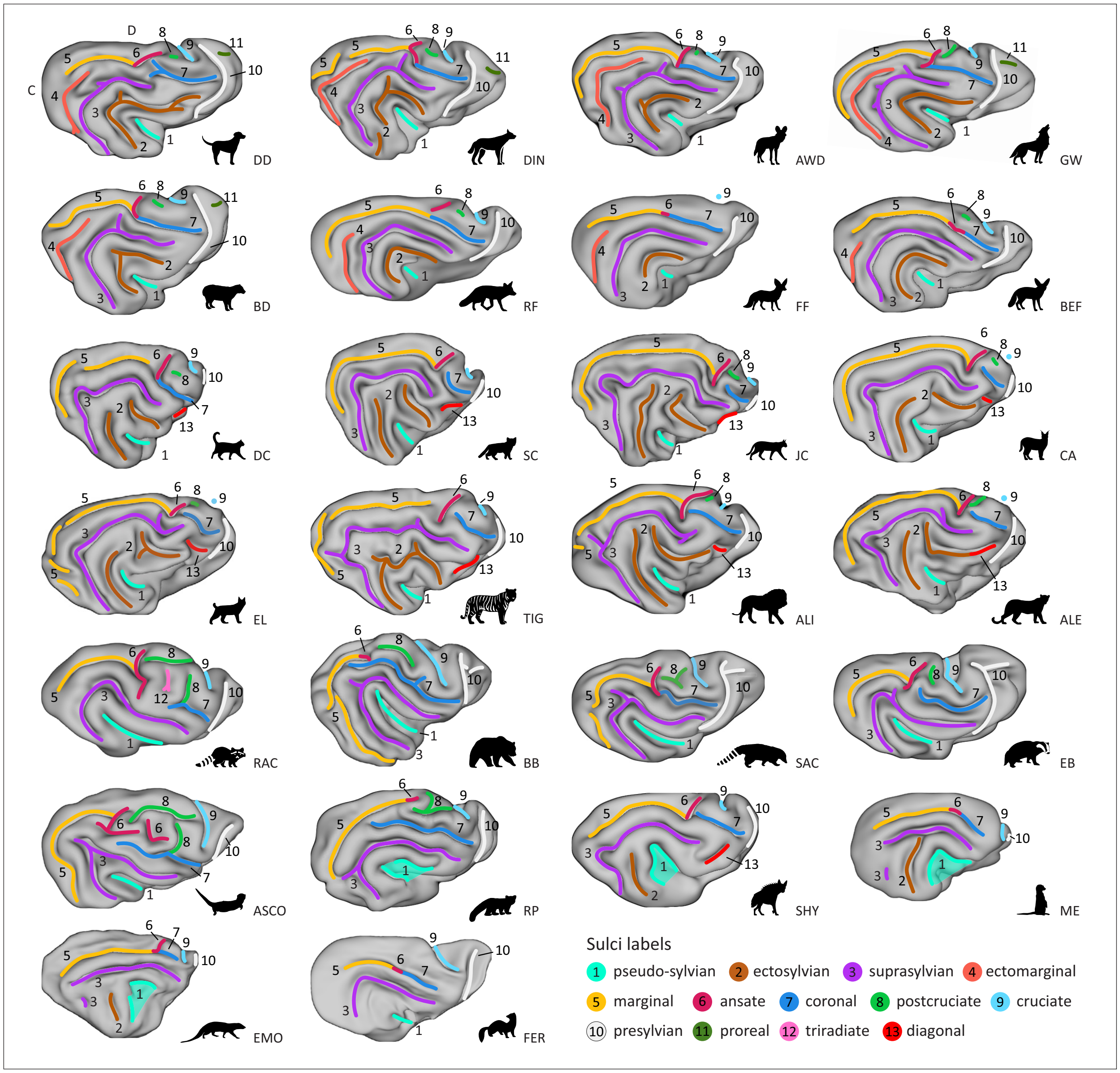

Figure 2. Lateral view showing variation of sulcal patterns across carnivorans. Surfaces are presented in descending order of sulcal complexity, starting with the canid brains that exhibited the highest number of unique major sulci. They are followed by felid brains which lacked the ectomarginal (orange, 4) and proreal (dark green, 11) sulcus but exhibited an additional diagonal (red, 13), and a split ectosylvian (brown, 2) sulcus, progressing towards species with the least complex sulcal topology. Despite exhibiting low sulcal complexity, the meerkat, Egyptian mongoose and striped hyaena had a caudal ectosylvian sulcus. The striped hyaena also exhibited a diagonal sulcus, analogous to Felids. All Arctoidea species in the fifth row, and the Asian small-clawed otter and red panda (sixth row, left) had complex or extended cruciate (light blue, 9), postcruciate (light green, 8) and ansate (purple red, 6) sulci. They also exhibited an inverted u-shaped suprasylvian sulcus compared to the arc shape observed in Canids and Felids (top four rows). We indicate the location of the cruciate sulcus with a blue dot if it is not well visible on the lateral surface due to its shape; see ***Figure 3*** for a dorsal view. Anatomical locations are indicated on the dog surface in the top row, left corner. C, caudal; D, dorsal. ALI, Asiatic lion; ALE, Amur leopard; ASCO, Asian small-clawed otter; AWD, African wild dog; BB, brown bear; BD, bush dog; BEF, bat-eared fox; CA, caracal; DC, domestic cat; DD, domestic dog; DIN, dingo; EB, Eurasian badger; EL, Eurasian lynx; EMO, Egyptian mongoose; FER, ferret; FF, fennec fox; GW, grey wolf; JC, jungle cat; ME, meerkat; RAC, raccoon; RF, red fox; RP, red panda; SAC, South American coati; SC, sand cat; SHY, striped hyaena; TIG, Bengal tiger.

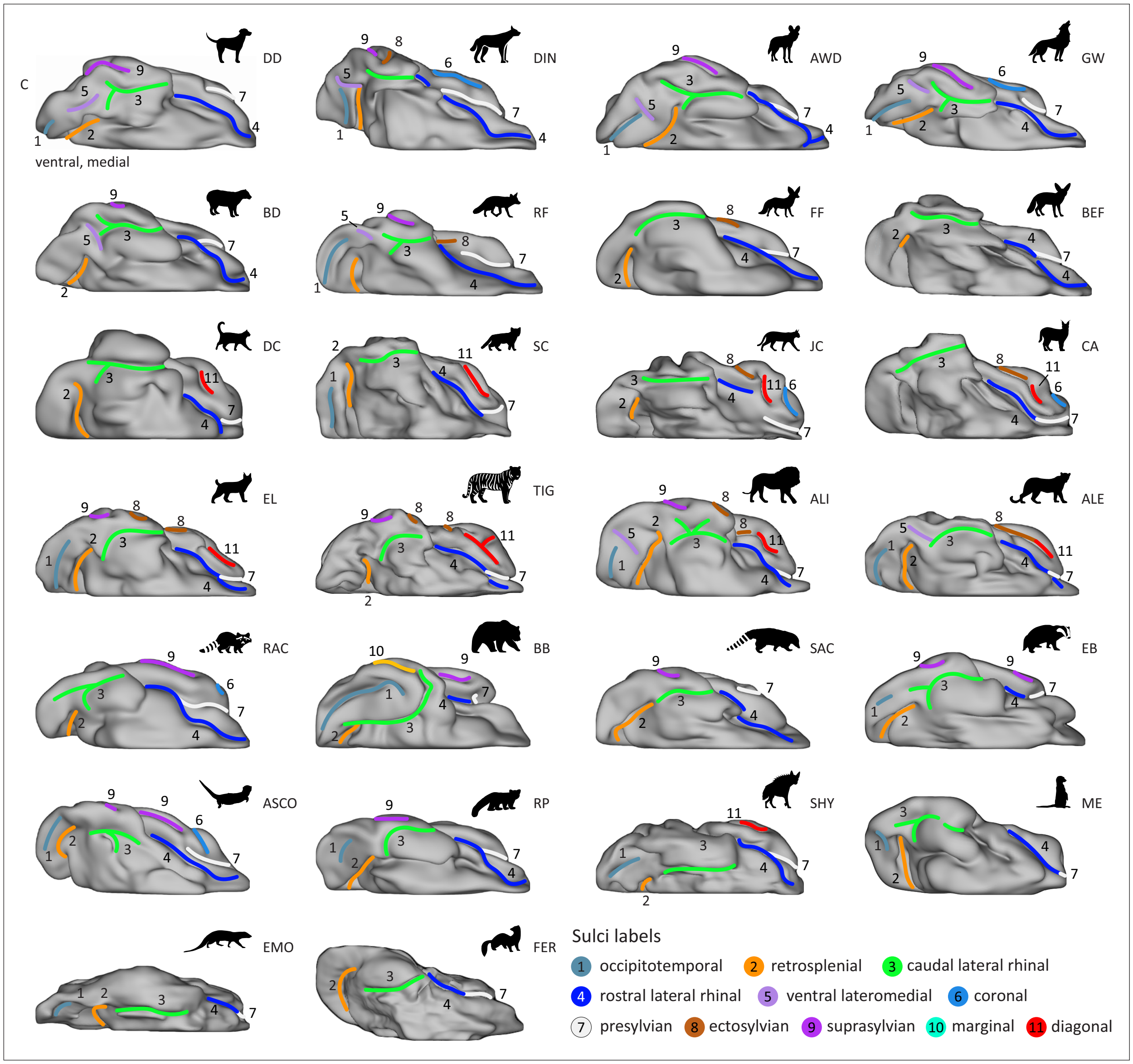

Figure 2—figure supplement 1. Ventral view of major neocortical sulci. The rostral and caudal rhinal fissure represent the ventral border of the carnivoran neocortex. The majority of the sulci visible on the ventral view can also be seen from a dorsal and/or lateral perspective (***Figures 2 and 3***), and the retrosplenial and occipitotemporal sulcus extend ventrally from the medial wall (see ***Figure 3—figure supplement 1***). The ventral lateromedial sulcus (5, pink) can only be seen on the ventral surface of the occipital lobe. We were not able to consistently identify this sulcus in all carnivoran species. Animal acronyms: ALI, Asiatic lion; ALE, Amur leopard; ASCO, Asian small-clawed otter; AWD, African wild dog; BB, brown bear; BD, bush dog; BEF, bat-eared fox; CA, caracal; DC, domestic cat; DD, domestic dog; DIN, dingo; EB, Eurasian badger; EL, Eurasian lynx; EMO, Egyptian mongoose; FER, ferret; FF, fennec fox; GW, grey wolf; JC, jungle cat; ME, meerkat; RAC, raccoon; RF, red fox; RP, red panda; SAC, South American coati; SC, sand cat; SHY, striped hyaena; TIG, Bengal tiger.

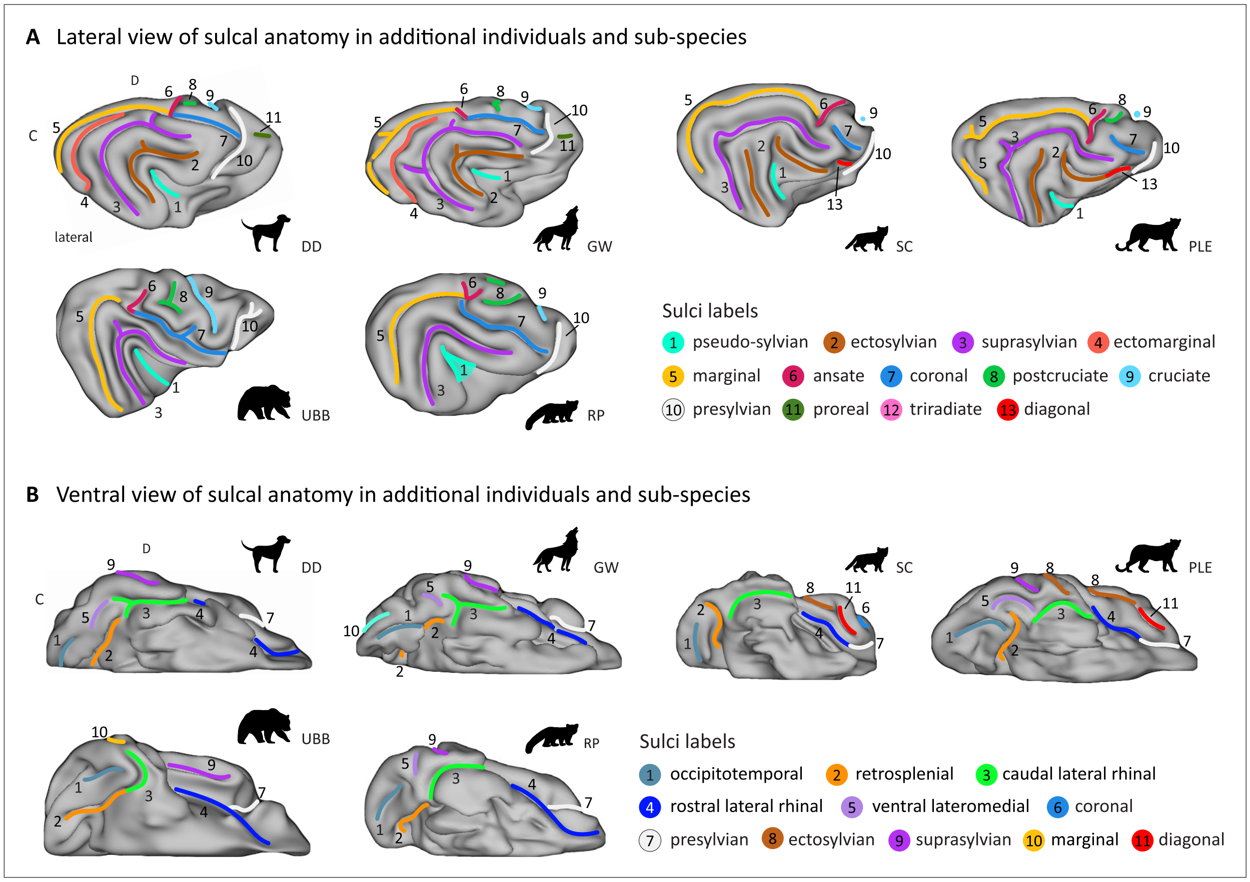

Figure 2—figure supplement 2. Lateral and ventral view of major neocortical sulci in additional individuals and sub-species. The sulcal topology of the additional individuals closely resembled the surfaces presented in the main text, with all major sulci present (see ***Figure 2***, ***Figure 2—figure supplement 1***). Only minor variations in sulcal shape were observed. (**A**) For example, u-shaped pseudo-sylvian fissure (cyan, 1) of the second red panda was continuous in contrast to the split configuration observed in the other specimen (***Figure 2***). (**B**) Similar to both brown bear specimens, the marginal sulcus of the second grey wolf was also visible from the ventral view. In contrast, this sulcus was not visible in the ventral view of the first grey wolf or in any of the other species examined. Animal acronyms: DD, domestic dog; GW, grey wolf; SC, sand cat; PLE, Persian leopard; UBB, Ussuri brown bear; RP, red panda.

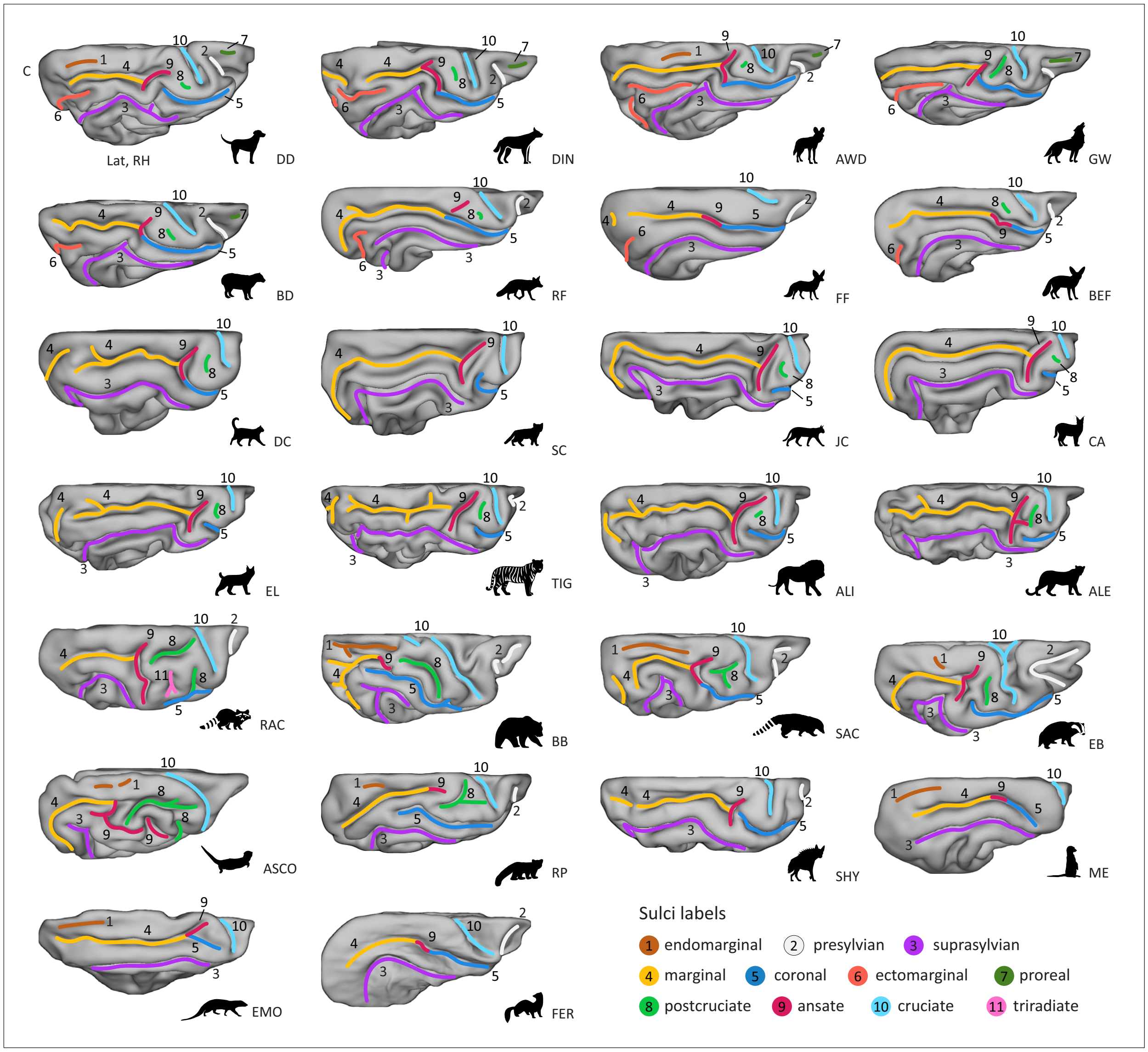

Figure 3. Dorsal view reveals varying complexity of sulci in parietal and frontal cortices across carnivoran families. Surfaces are presented in descending order of sulcal complexity, starting with brains exhibiting the most complex sulcal topology and progressing to those with the least, as in ***Figure 2***. Only the wolf-like Canids (top row) and the bush dog (second row, left) had a proreal sulcus (green, 7). The brown bear had a secondary cruciate sulcus (light blue, 10). Anatomical locations are indicated on the domestic dog surface in the top row, left corner. Lat, lateral; C, caudal; RH, right hemisphere. ALI, Asiatic lion; ALE, Amur leopard; ASCO, Asian small-clawed otter; AWD, African wild dog; BB, brown bear; BD, bush dog; BEF, bat-eared fox; CA, caracal; DC, domestic cat; DD, domestic dog; DIN, dingo; EB, Eurasian badger; EL, Eurasian lynx; EMO, Egyptian mongoose; FER, ferret; FF, fennec fox; GW, grey wolf; JC, jungle cat; ME, meerkat; RAC, raccoon; RF, red fox; RP, red panda; SAC, South American coati; SC, sand cat; SHY, striped hyaena; TIG, Bengal tiger.

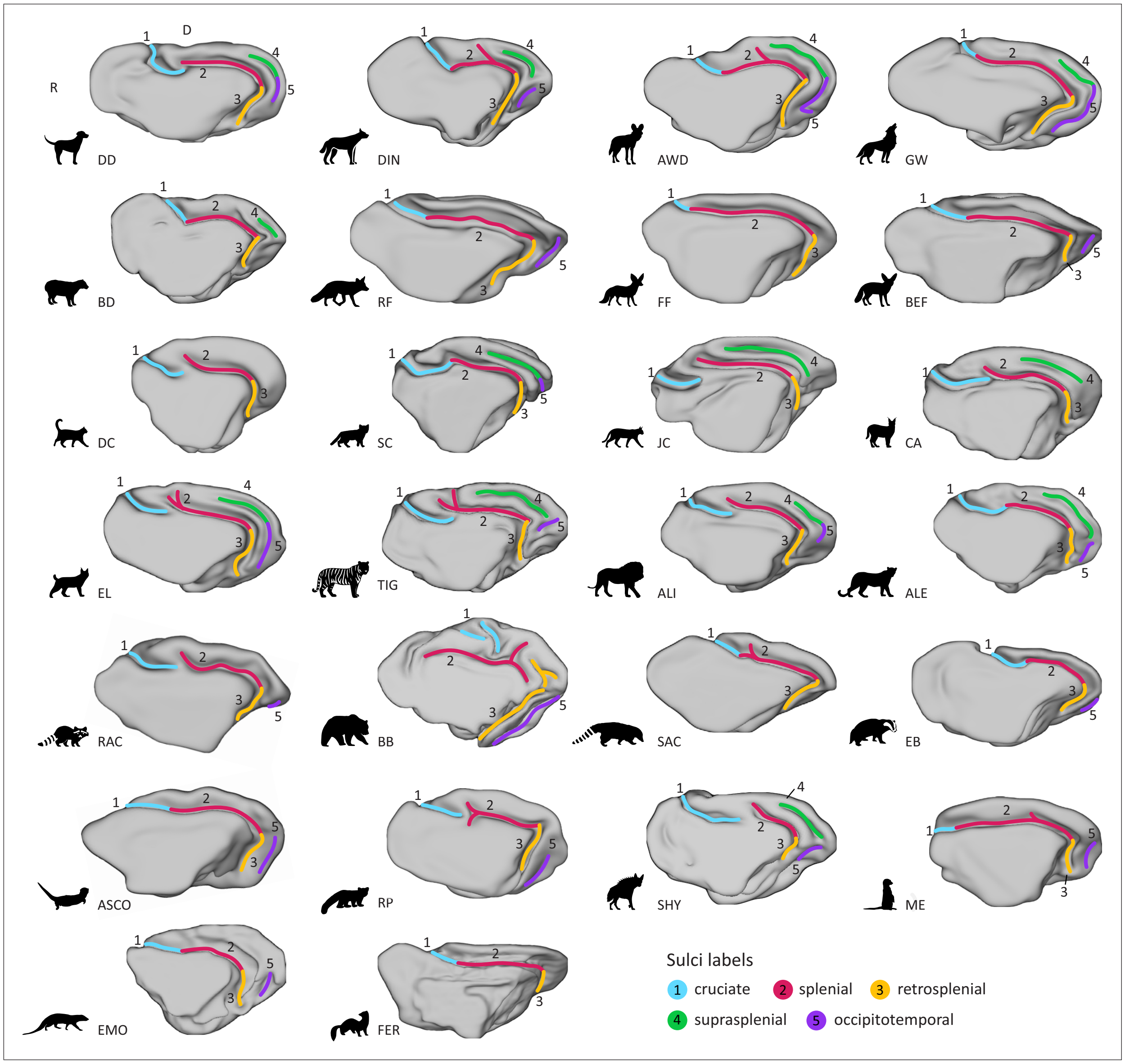

Figure 3—figure supplement 1. Major neocortical sulci in the medial wall. The cruciate sulcus (light blue, 1) was the only sulcus that was also visible on the lateral and dorsal view (see ***Figures 2 and 3***). All species had a cruciate, splenial (purple red, 2), and retrosplenial (yellow, 3) sulcus. Occurrence and appearance of the suprasplenial (green, 4) and occipitotemporal (purple, 5) sulci varied across species. Anatomical locations are indicated on the domestic dog surface in the top row, left corner. R, rostral; D, dorsal. Animal acronyms: ALI, Asiatic lion; ALE, Amur leopard; ASCO, Asian small-clawed otter; AWD, African wild dog; BB, brown bear; BD, bush dog; BEF, bat-eared fox; CA, caracal; DC, domestic cat; DD, domestic dog; DIN, dingo; EB, Eurasian badger; EL, Eurasian lynx; EMO, Egyptian mongoose; FER, ferret; FF, fennec fox; GW, grey wolf; JC, jungle cat; ME, meerkat; RAC, raccoon; RF, red fox; RP, red panda; SAC, South American coati; SC, sand cat; SHY, striped hyaena; TIG, Bengal tiger.

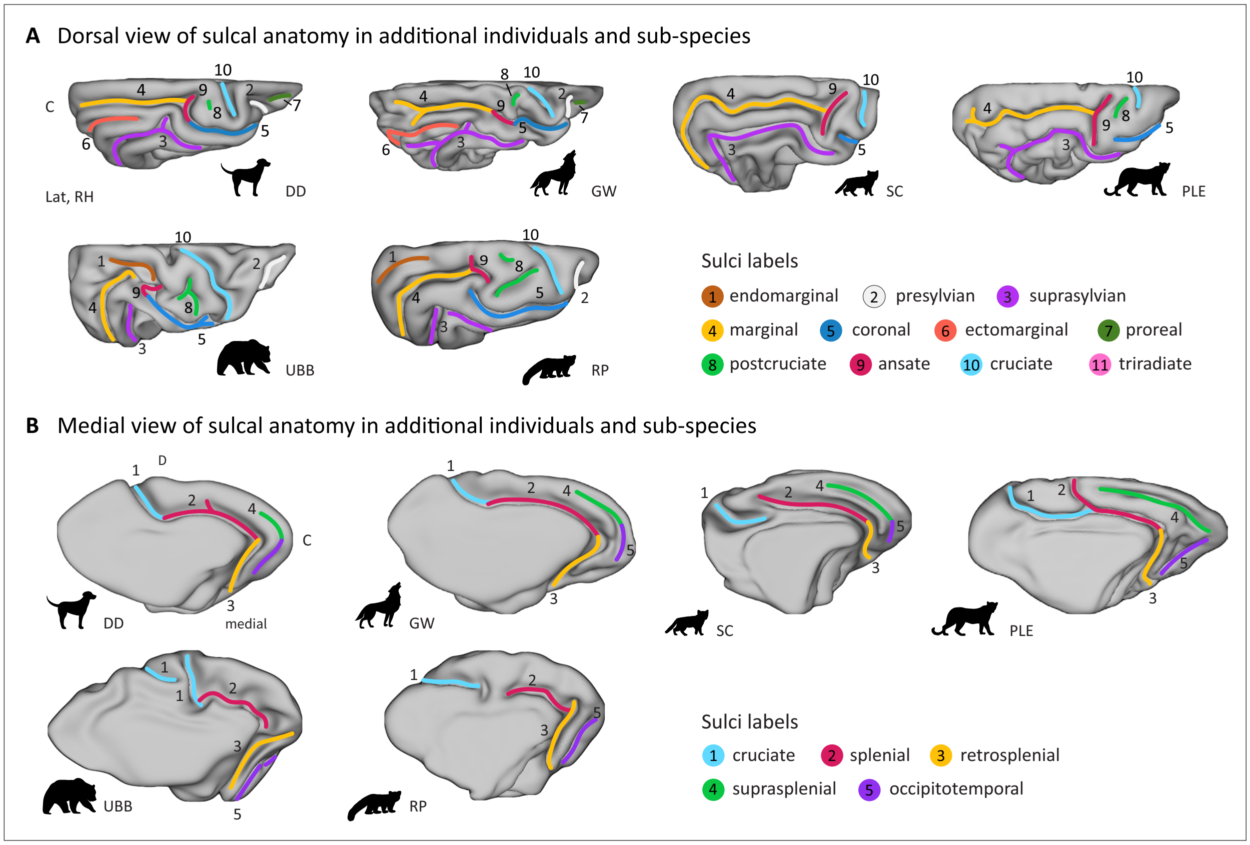

Figure 3—figure supplement 2. Dorsal and medial view of major neocortical sulci in additional individuals and sub-species. None of the supplementary samples revealed major variations in shape or presence of the sulcus; only minor variations in sulcal shape were observed. (**A**) For example, in the Ussuri brown bear (UBB), the ansate sulcus (purple, 9) was more clearly identifiable than in the brown bear, as it displayed the typical perpendicular orientation relative to the marginal sulcus. (**B**) In the second sand cat, the cruciate (light blue, 1) and splenial (purple red, 2) sulci were detached, a variation also observed in several other species (Figure 3—figure supplement 2) whereas in the first sand cat, these sulci were merged. Animal acronyms: DD, domestic dog; GW, grey wolf; SC, sand cat; PLE, Persian leopard; UBB, Ussuri brown bear; RP, red panda.

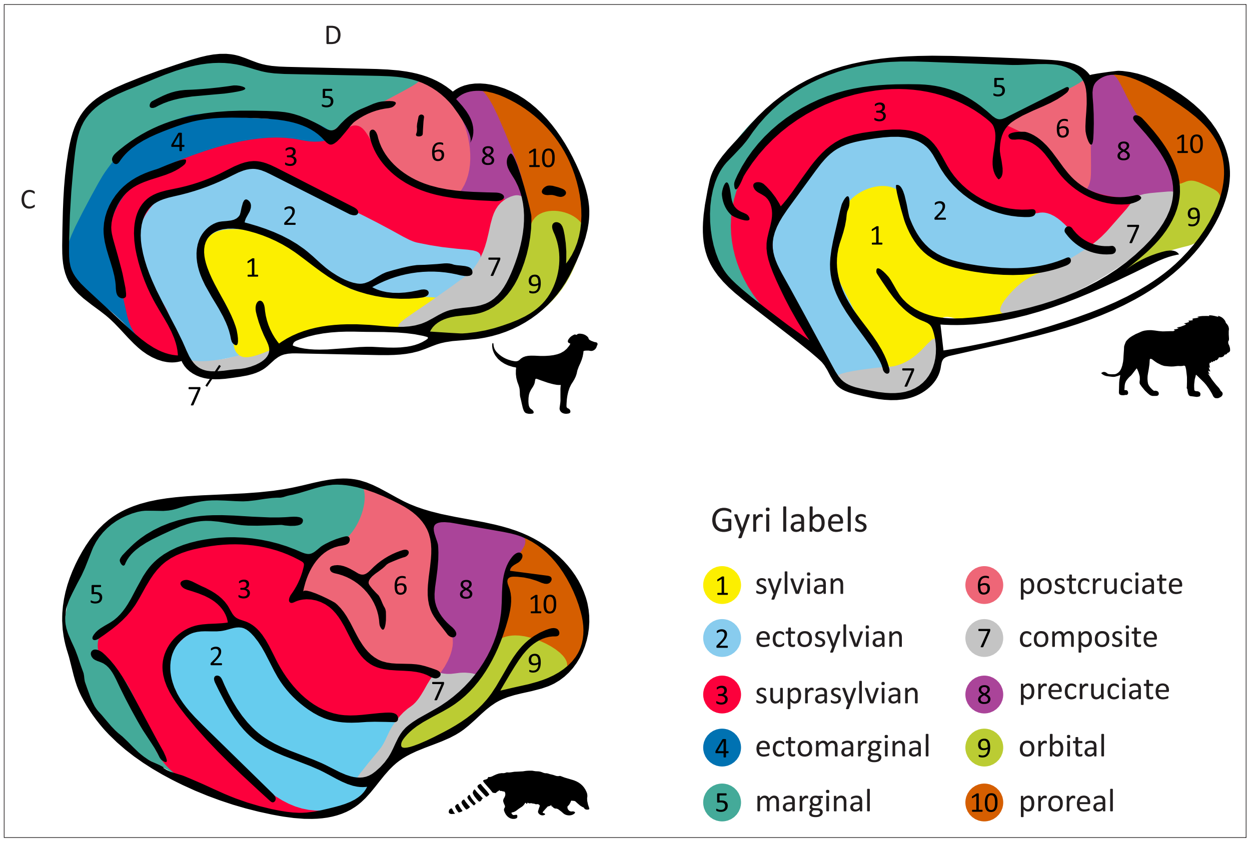

Figure 4. Sulcal anatomy variations and corresponding gyral differences. As illustrated on the lateral view of the domestic dog brain (upper left corner), only Canidae have an ectomarginal gyrus (dark blue). Additionally, Canidae and Felidae (Asiatic lion, upper right corner) species have an (incomplete) sylvian gyrus (yellow). Species exhibiting a more complex postcruciate sulcus have an expanded postcruciate gyrus (light red) as illustrated on the South American coati brain (lower left corner). Nomenclature follows prior descriptions in Canidae and Felidae (***Czeibert et al., 2019***; ***Pakozdy et al., 2015***; ***Rogers Flattery et al., 2023***; ***Stolzberg et al., 2017***), and descriptions of the ferret brain for species lacking an ectosylvian sulcus (***Radtke-Schuller, 2018***). The rostral suprasylvian gyrus (red) is also called the coronal gyrus in ferrets, and in the field of paleoneurology, post- and precruciate gyri (light red, purple) are often referred to as the posterior and anterior sigmoid gyrus (see e.g., ***Lyras et al., 2023***). White space indicates allocortex. C, caudal; D, dorsal.

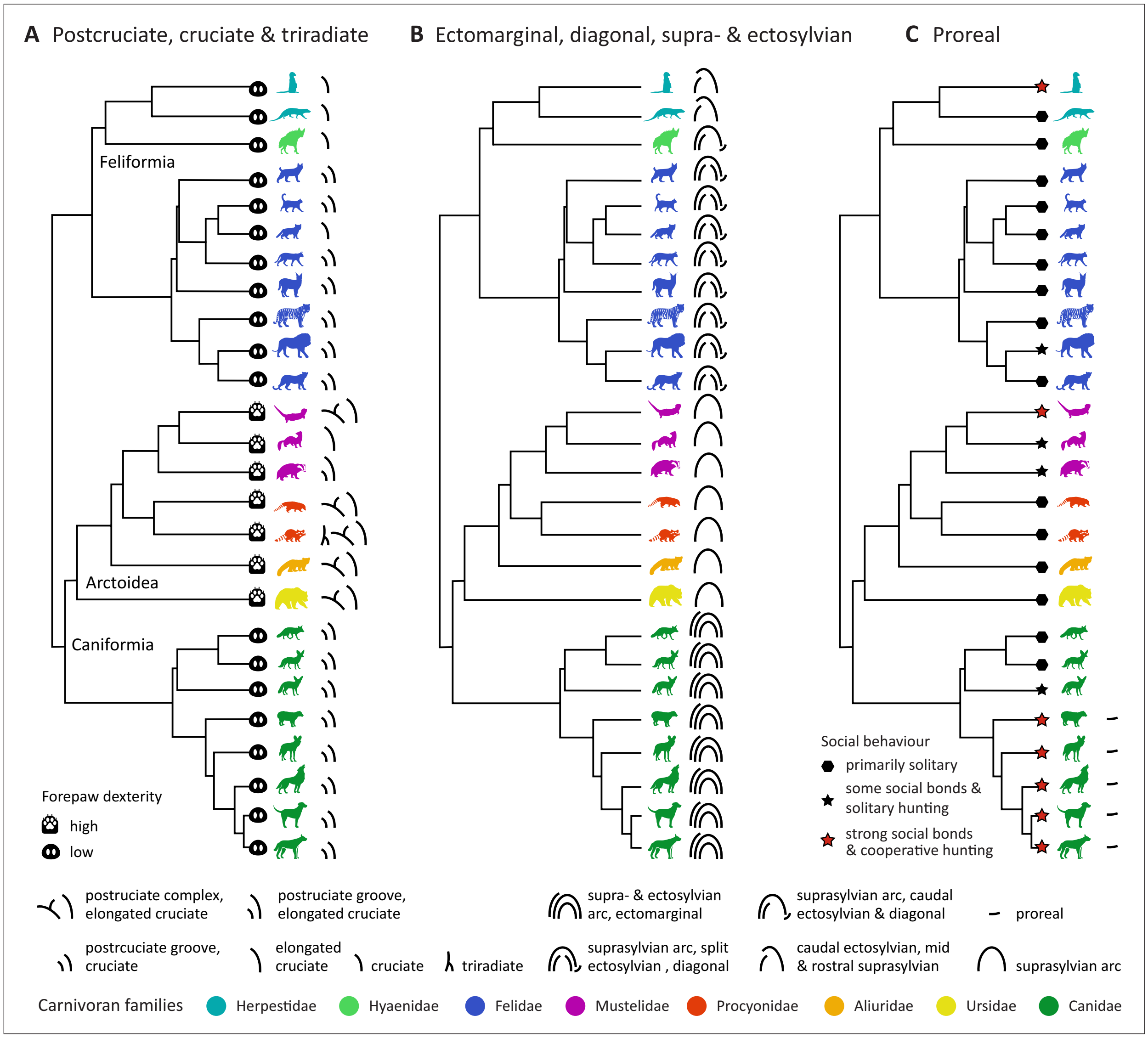

Figure 5. Lineage-specific observations and potential functional correlates. (**A**) The Arctoidea species with complex sulcal configurations in the somatosensory cortex also exhibit more pronounced forepaw dexterity (see e.g., ***Iwaniuk et al., 1999***; ***Iwaniuk and Whishaw, 1999***; ***Radinsky, 1968***). In the red panda, coati, and raccoon, this potentially expanded cortical territory surrounding the postcruciate sulcus or complex appears to accommodate the primary somatosensory cortex, with a significant representation of the forepaw (see ***Figure 6***). (**B**) Canids had the most complex occipitotemporal sulcal anatomy, followed by felids and the herpestids and striped hyaena with a unique sulcal configuration. This might indicate the expansion of auditory and visual regions in canids and of auditory regions in felids (see ***Figure 6***). Arctoidea species exhibited the least complex occipitotemporal sulcal topology. (**C**) All canids with strong social bonds and that engage in cooperative hunting (***Macdonald and Sillero-Zubiri, 2004***; ***Wilson and Mittermeier, 2009***; ***Wilson, 2000***) had an additional sulcus in the frontal lobe, the proreal sulcus. Complementary quantitative analyses confirmed a positive association between sociality and proreal sulcus length, and between forepaw dexterity and the length of the postcruciate and cruciate sulci (***Figure 5—figure supplement 1***).

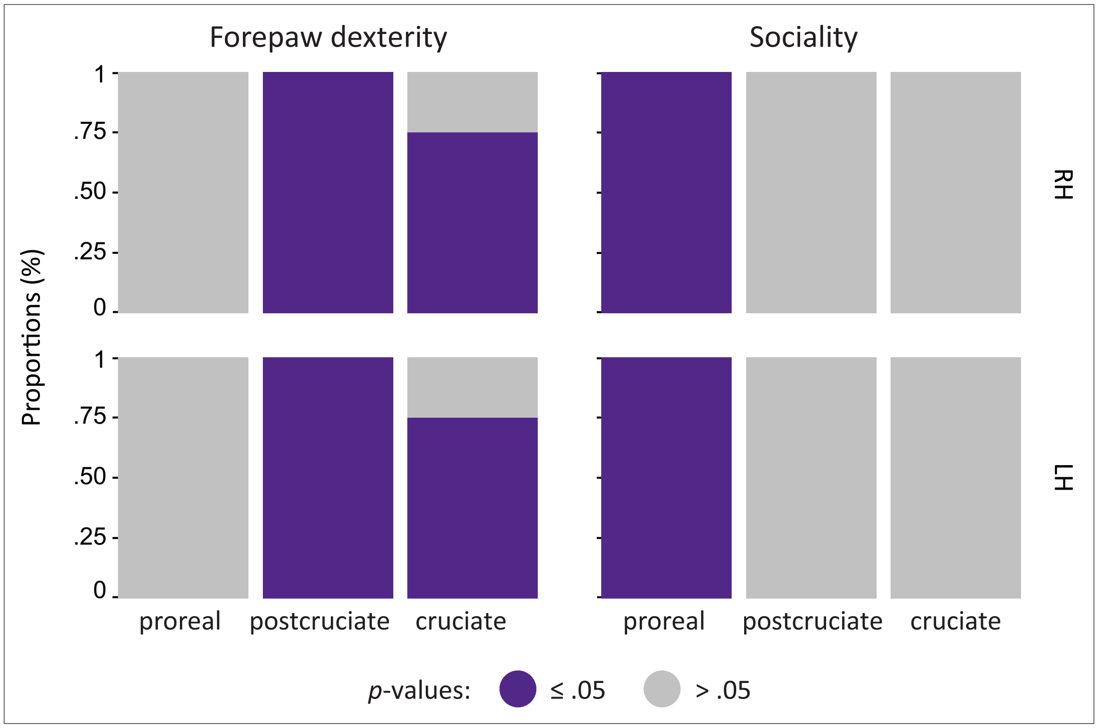

Figure 5—figure supplement 1. Proportion of significant associations between relative sulcal length and behavioural characteristics. Preliminary quantitative analyses, conducted to complement qualitative descriptions (***Figure 5***), reveal that the relative length of the proreal sulcus was consistently greater in cooperatively hunting species than in solitary hunters regardless of choice for reference sulcus ($n = 7$) and both hemispheres, while no effect of forepaw dexterity was observed (***Figure 5—source data 1***). In contrast, analyses of the postcruciate sulcus revealed the opposite pattern, with consistently greater sulcal length in species with high forepaw dexterity across all reference sulci ($n = 4$) and in both hemispheres, and no significant relationship with sociality (***Figure 5—source data 2***). Analyses of the cruciate sulcus length ($n = 4$ reference sulci) revealed a positive relationship with high forepaw dexterity in 75% of models in each hemisphere, but no significant relationship with sociality (***Figure 5—source data 3***). RH, right hemisphere; LH, left hemisphere.

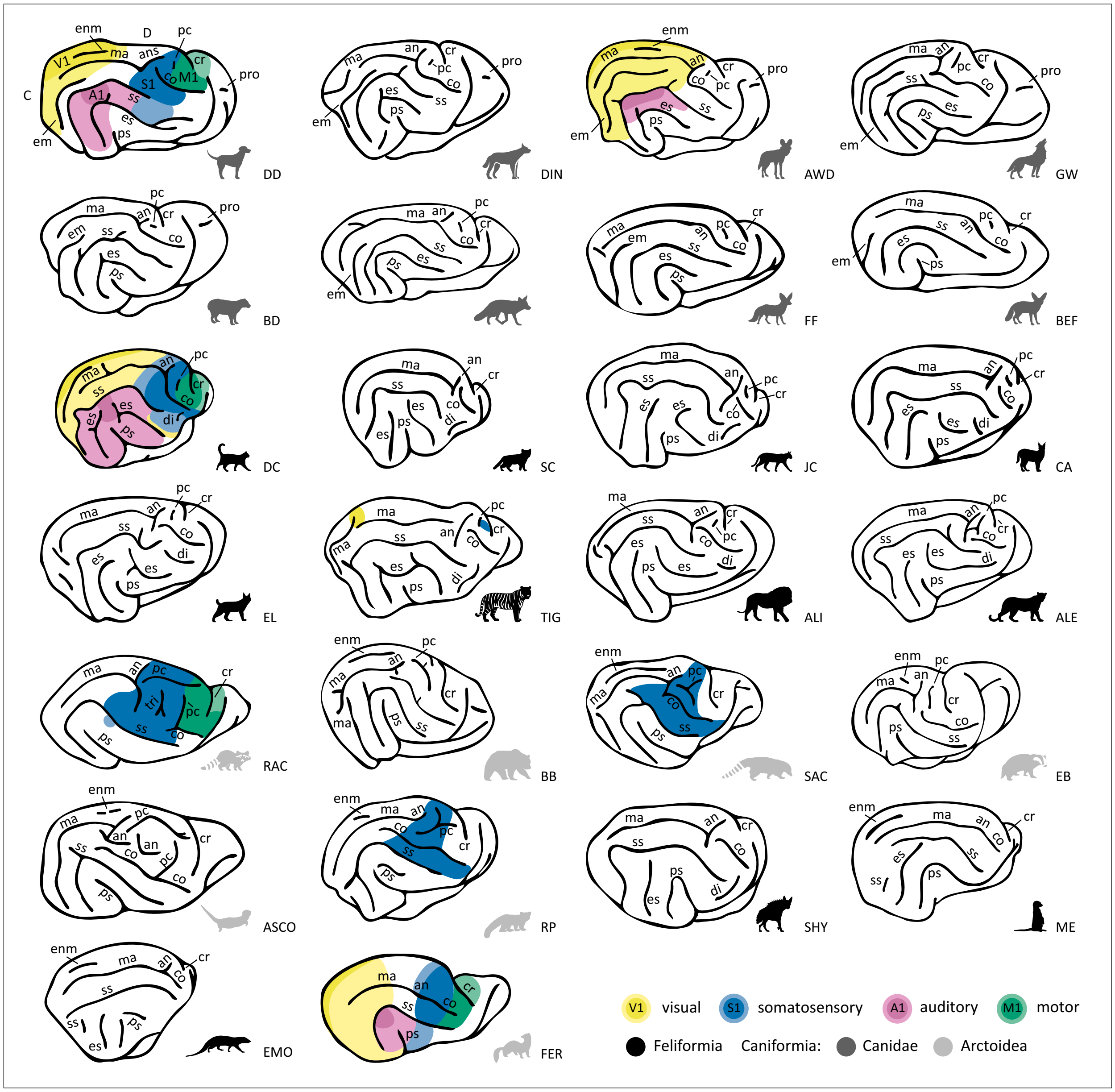

Figure 6. Schematic overview of cortical sulcal anatomy and available information about cortical sensory areas. While knowledge of the sensory regions in carnivoran brains is still limited, the best-understood brains of the species in our sample were the domestic cat (third row, left) and ferret (bottom row, right) followed by the domestic dog (top row, left). Based on prior electrophysiological, histological, and neuroimaging research (e.g., ***Boch et al., 2021***; ***Chengetanai et al., 2020a***; ***Douglas Jameson et al., 1968***; ***Guran et al., 2024***; ***Hardin et al., 1968***; ***Johnson et al., 2016***; ***Kosmal, 2000***; ***Law et al., 1988***; ***Manger et al., 2002***; ***Mclaughlin et al., 1998***; ***Radtke-Schuller et al., 2020***; ***Stolzberg et al., 2017***; ***Tunturi, 1944***; ***Welker and Campos, 1963***), we indicate approximate locations of unimodal sensory cortices on a lateral view of the brains of these species. Darker shades indicate primary sensory cortices, including the primary visual (V1, yellow), auditory (A1, pink), motor (M1), and somatosensory (S1) cortex. Lighter shades mark higher-order unimodal sensory regions. White spaces indicate that these regions have not been investigated yet, or research to date has revealed inconclusive results. It is, for example, possible that the African wild dog has additional auditory regions located ventral to those identified (***Chengetanai et al., 2020a***). C, caudal; D, dorsal. Sulcus acronyms: an, ansate; co, coronal; cr, cruciate; di, diagonal; em, ectomarginal; enm, endomarginal; es, ectosylvian; ma, marginal; pr, postcruciate; pro, proreal; ps, pseudo-sylvian; ss, suprasylvian; tri, triradiate. Animal acronyms: ALI, Asiatic lion; ALE, Amur leopard; ASCO, Asian small-clawed otter; AWD, African wild dog; BB, brown bear; BD, bush dog; BEF, bat-eared fox; CA, caracal; DC, domestic cat; DD, domestic dog; DIN, dingo; EB, Eurasian badger; EL, Eurasian lynx; EMO, Egyptian mongoose; FER, ferret; FF, fennec fox; GW, grey wolf; JC, jungle cat; ME, meerkat; RAC, raccoon; RF, red fox; RP, red panda; SAC, South American coati; SC, sand cat; SHY, striped hyaena; TIG, Bengal tiger.