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Domesticating olfaction: Dog breeds, including scent hounds, have reduced cribriform plate morphology relative to wolves

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Abstract

The domestic dog is assumed by nearly everyone to be the consummate smeller. Within the species *Canis familiaris* individual breeds, such as the bloodhound or beagle, are known as olfactory stars. These are "scent breeds," a grouping variably defined as a genetic clade or breed class commonly used for scent detection tasks. Previous work suggests that the dog has a more robust olfactory anatomy than many mammal species. Now we undertake a closer investigation of the dog's olfactory system, both in relationship to its closest wild relatives, the wolf and coyote, and across individual breeds. First, we seek to resolve whether the dog has lost olfactory capacity through its domestication from the wolf lineage. Second, we test the inertial lore that among dogs, "scent breeds," have a superior olfactory facility. As a measure of relative olfactory capacity, we look to the cribriform plate (CP), a bony cup in the posterior nasal cavity perforated by passageways for all olfactory nerve bundles streaming from the periphery to the brain. Using high-resolution computed tomography (CT) scans and digital quantification, we compare relative CP size in 46 dog breeds, the coyote and gray wolf. Results show the dog has a reduced CP surface area relative to the wolf and coyote. Moreover, we found no significant differences between CP size of "scent" and "non-scent" breeds. Our study suggests that the dog lost olfactory capacity as a result of domestication and this loss was not recovered in particular breed groupings through directed artificial selection for increased olfactory facility.

KEYWORDS

cribriform plate, domestication, domestic dog, olfaction, scent breed

1 | INTRODUCTION

Ask anyone which animal has the keenest sense of smell. Chances are the answer will be, "The dog!" Some may even offer a specific breed, "The bloodhound!" The olfactory lore surrounding domestic dogs is far-reaching. The dog's olfactory powers have been inflated to superhero status by everyone from breeders to popular figures such as Sir Arthur Conan Doyle and his Sherlock Holmes (Anderson, 2018; Doyle, 1904; Ferguson, 2019). However, quite apart from all lore, the genuine feats of working scent detection dogs suggest that human's best friend possesses a relatively strong sense of smell. Indeed, in studies measuring olfactory receptor (OR) gene repertoires, olfactory epithelium surface area, and odorant discrimination ability in mammals, the domestic dog consistently ranks relatively high among sampled species (Lauruschkus, 1942; Marshall, Blumer, & Moulton, 1981; Niimura, Matsui, & Touhara, 2014; Pihlström, Fortelius, Hemilä, Forsman, & Reuter, 2005). Moreover, a recent study comparing the relative expansion and loss of olfactory anatomy across mammals found that dogs have larger olfactory skull morphology, specifically the cribriform plate (CP), than all but 5 of 27 species sampled (Bird et al., 2018) (see Figures 1,2). As working animals, dogs play a central role in critical detection tasks, sniffing out chemical indicators of cancer, low insulin levels in diabetics, drugs and explosives, rare species, human remains, and potentially COVID-19 (Gazit & Terkel, 2003; Horvath, Andersson, & Nemes, 2013; Jendrny et al., 2020; Komar, 1999; Rooney, Morant, & Guest, 2013), making the dog the only animal aside from the rat (Poling, Weetjens, Cox, Beyene, & Sully, 2010) to be employed for this kind of work.

Missing from these comparative olfactory studies and surveys mentioned above is the evolutionary history of the dog, specifically its relationship to the wolf and its intraspecific divergence into breeds. Since its initial domestication from the gray wolf lineage more than 15,000 years ago (Freedman et al., 2014; Sablin & Khlopachev, 1997), the dog has been the object of artificial selection. From the mid-19th century forward, selection was formalized to produce the nearly 400 (and counting) extant, phenotypically divergent breeds (Crowley & Adelman, 1998; Parker et al., 2017; vonHoldt et al., 2010). Here we undertake a closer investigation of the dog's olfactory system, both in relationship to its closest wild relatives, the wolf and the coyote, and intraspecifically across breeds. First, we seek to resolve whether the dog has lost olfactory capacity through the process of its domestication from the gray wolf. Second, we investigate whether any breed or breed grouping distinguishes itself as having olfactory anatomy that is particularly expanded or reduced.

Almost certainly, extant domestic dogs are less reliant than wild canids on olfaction for their existence. In general, domestic dogs are not active hunters and instead rely on food and shelter provided by humans. Even poorly treated village dogs probably do not travel far for their food and have little need for long-distance detection of potential prey or predators. It is difficult to know how and when dogs became so dependent on humans for food. Perhaps the most common hypothesis is that early in the dog's domestication, founder populations of less fearful wolf individuals, and later proto-dogs, lived commensally with early nomadic humans and scavenged human food scraps (Driscoll, Macdonald, & Brien, 2009; Germonpré, Lázničková-Galetová, Sablin, & Bocherens, 2018; Müller, 2005). Supporting this scenario is a genomic analysis indicating that by at least 7,000 years ago dogs had acquired adaptations in their digestive enzymes for a diet much richer in starch than that of the carnivorous wolf (Axelsson, Ratnakumar, Arendt, Maqbool, Webster, Perloski, Liberg, Arnemo, Hedhammar & Lindblad-Toh, 2013). In addition, archaeological evidence and stable isotope analysis from the ca. 7,000-year-old Namu site in British Columbia have revealed that coexisting humans and dogs shared the same seasonally fluctuating food sources (Cannon, Schwarcz & Knyf, 1999). Together, these data document an ecological shift in the dog relative to the wolf away from predation, and toward a dietary regime that involved a smaller home range and reduced selection pressure on the olfactory system. Consequently, we expect that the dog's olfactory system will be reduced on average relative to that of their ancestor, the gray wolf.

Despite the dietary shift and possibly attendant olfactory loss in early dogs, it is conceivable that in more recent history, humans directly bred for an expansion of olfactory capacity in certain domestic dog types and that consequently those breeds might exhibit an olfactory apparatus more similar to that of the gray wolf. We might expect this, as humans have been remarkably successful in breeding phenotypic diversity in dogs through artificial selection. As early as 4,000 years ago dogs displayed disparate morphologies suitable for select functions, such as herding and guarding (Bostock, 1855; Osborn and Osbornová, 1998). More recently, concerted breeding has amplified such differences by selecting for phenotypic traits that either satisfy preferences for appearance or improve performance in specific functional tasks, such as racing or fighting (Caius, 1576; Kemp, Bachus, Nairn, & Carrier, 2005). Scent tracking ability is considered to be a functional trait directly selected for in particular breeds for the specific task of hunting. Indeed, a common claim by breeders, kennel clubs, and dog owners alike is that scent breeds have a particularly sensitive nose as a result of directed breeding (Brey & Reed, 1978; Crowley & Adelman, 1998, https://www.akc.org/dog-breeds/english-foxhound/). If we take this as our assumption, we might expect scent breeds to display a relatively large CP relative to other breeds. By contrast, breeds selected for visual acuity (sight breeds), such as the borzoi, or short snouts (brachycephalic breeds), might be expected to show reductions in olfactory anatomy relative to scent breeds, due to constraints imposed by sensory trade-offs or cranial morphology, respectively. To test for significant differences in olfactory morphology among dogs, particularly scent and sight breeds, we quantified olfactory skull anatomy across individual dog breeds and larger breed groupings. Finally, we explored whether the breed grouping labeled “ancient” dogs has an expanded olfactory skeleton relative to other dog breed groupings. The “ancient” dog grouping is defined in the literature as being genetically divergent from all other (modern) dog breeds and includes breeds (among others, basenji, dingo, Siberian husky) that originated from ancient cultures more than 500 years ago (American Kennel Club, 2006; Freedman et al., 2014; Parker et al., 2017; vonHoldt et al., 2010; Wilcox & Walkowicz, 1989). As some breeds within the “ancient” grouping have experienced admixture with wolves subsequent to their breed origins (vonHoldt et al., 2010), we investigated whether “ancient” group dogs retain the signature of a larger, ancestral olfactory capacity relative to modern breeds.

To examine the impact of domestication and concerted artificial selection on the olfactory capacity of the domestic dog, we used a single metric of olfactory anatomy, the surface area of the CP. The CP is a perforated cup of bone in the posterior nasal cavity that separates the peripheral olfactory anatomy from the central nervous system and houses the olfactory bulb (Negus, 1958). The foramina in the CP bone usher olfactory nerves on their path from the olfactory epithelium in the snout to the brain (Figure 1a–c). The CP is the only entry point for axon bundles from olfactory sensory neurons to reach the olfactory bulb. We chose the CP for four reasons. First, its size covaries with the relative amount of peripheral olfactory innervation present in a mammal's nasal chamber (Pihlström et al., 2005); therefore, quantifying its surface area allows us to gauge and compare relative levels of olfactory investment across domestic dog breeds and their closest wild relatives. Second, an earlier study looking across all mammal superorders found that relative CP size (RelCP) is closely correlated with the number of OR genes in a species' genome, establishing the CP as a metric of the evolutionary expansions and losses in mammalian olfactory systems (Bird et al., 2018). Furthermore, CP surface area correlates closely with surface area of

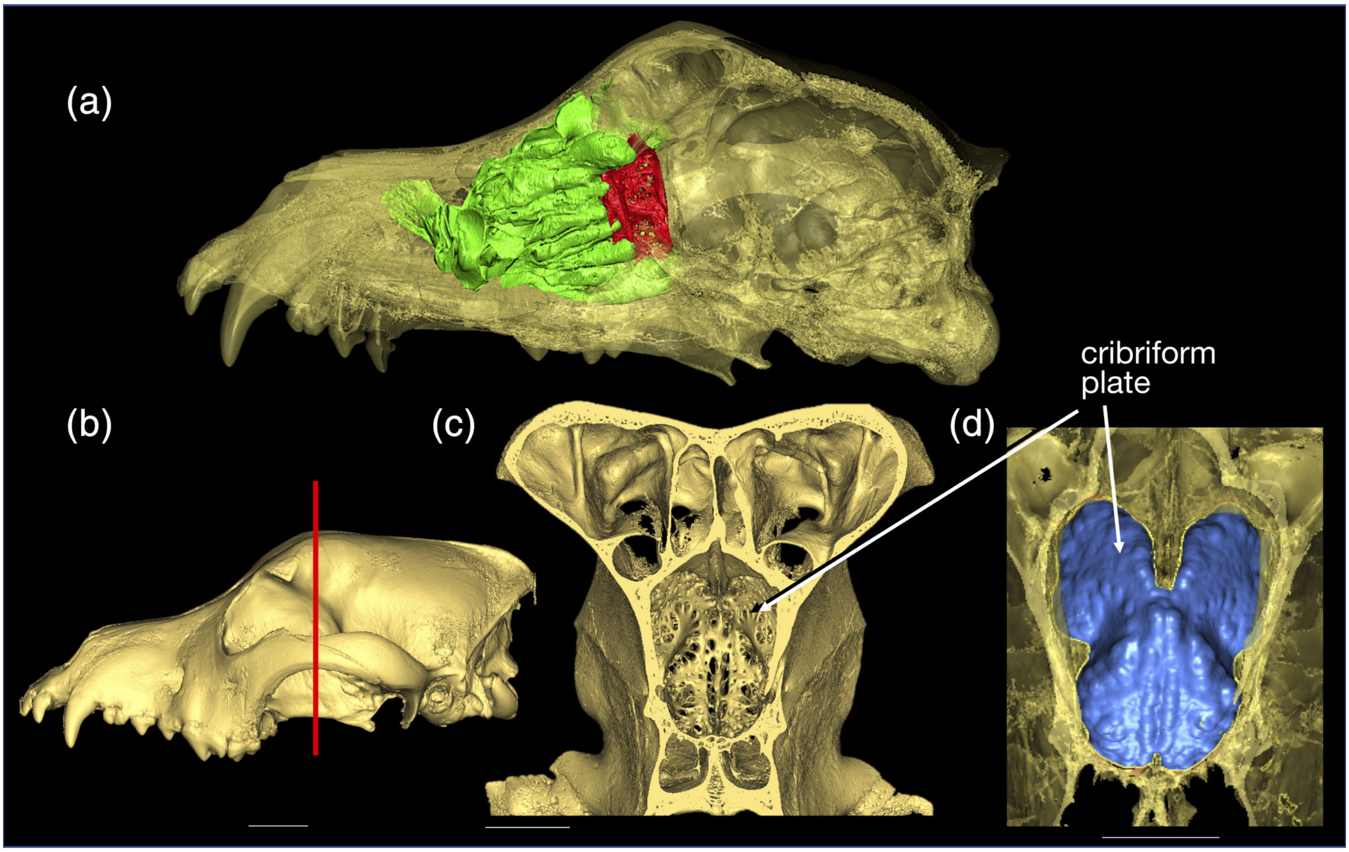

FIGURE 1 Nasal anatomy and surrounding skull morphology in the domestic dog (American pit bull breed) as viewed from 3D digital models constructed from CT scans in Mimics. (a) Transparent 3D model of dog skull viewed in lateral-oblique aspect. Green, ethmoid and frontal turbinals; red, cribriform plate. (b) Lateral view of skull model. Red line, location of transverse section as seen in (c). Scale bar, 20 mm. (c) Cribriform plate (CP) with myriad foramina for olfactory nerves, as viewed from the brain case in posterior aspect. Scale bar, 10 mm. (d) Blue, CP surface after foramina have been digitally filled. The surface describing only the perforated area is digitally incised and the area is calculated in Mimics. The skull matrix is rendered transparent to better view the concave and partially occluded CP surface. Scale bars, 10 mm

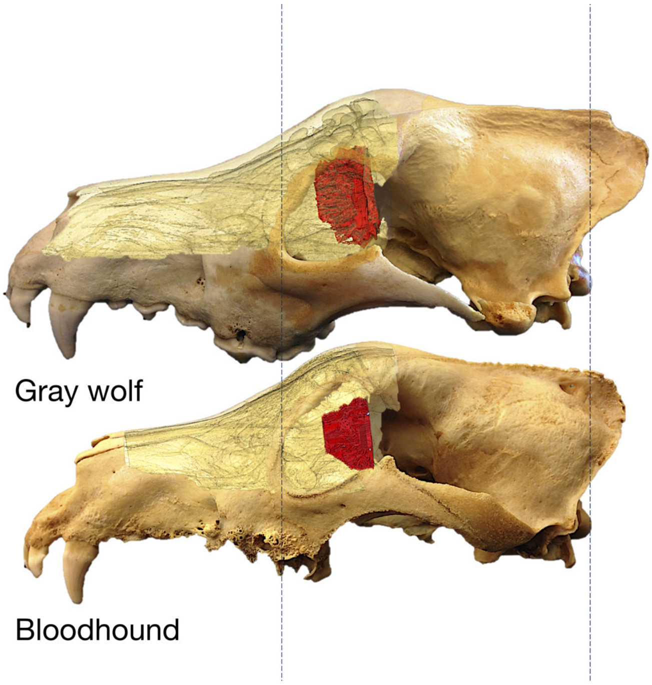

FIGURE 2 Cribriform plate morphology in the gray wolf and domestic dog (bloodhound breed). Digital 3D models of the cribriform plates in red within digital skull matrix is superimposed onto photographs of the wolf and bloodhound. The distance between the dashed lines is the occiput to orbit length (OOL), the metric for body size used in this article. See Figure 3 for comparison of wolf and bloodhound relative CP area. Wolf and bloodhound skulls courtesy of the National Museum of Natural History and Yale Peabody Museum

another olfactory skull feature, the olfactory (ethmoid and frontal) turbinal bones, which carry the olfactory epithelium (Bird, Amirkhanian, Pang, & Van Valkenburgh, 2014) (Figure 1a,d). Finally, because it is an osseous feature and can be quantified in some fossil skulls (Bird et al., 2018), the CP can be applied as an informative metric to infer relative olfactory capacity in prehistoric wolves and proto dogs found at Pleistocene and Holocene archaeological sites (Sablin & Khlopachev, 1997). Below we present the first comparative, quantitative investigation of olfactory skeleton morphology in the gray wolf and 46 breeds of its domesticated dog descendants.

2 | MATERIALS AND METHODS

2.1 | Specimens sampled

We sampled 103 skulls from 45 dog breeds, one unknown breed, and two species of wild canid, gray wolf (*Canis lupus*) and coyote (*Canis latrans*) (Table 1). All specimens were sourced from museum and university collections listed in Table 1. Availability permitting, we sampled two adult specimens, preferably one male and one female, for each dog breed or wild canid species. Most of our sample is comprised of dogs whose breed identities were assigned by the collectors, and nine dogs were documented show breeds. One dog specimen collected from an archaeological site on an unspecified Channel Island off Southern California is designated here as "unknown breed," as dogs found in former Native American dwelling sites on the Channel Islands have not been designated as a discrete breed (Rick et al., 2008). Sampled wild canid species include only wild caught adult specimens. Species and breed body masses, as estimated from the literature (Crowley & Adelman, 1998; Nowak, 1999), ranged from approximately 2.25 to 66 kg.

2.2 | Breed groupings

We used two separate criteria for classifying the domestic dogs into breed groupings. First, to determine whether there are significant differences in RelCP size between scent breeds and non-scent breeds, and between ancient and modern breeds, we grouped the breeds into (a) scent breeds (Ensminger, 2011; Parker et al., 2017; Rocznik et al., 2015; vonHoldt et al., 2010), (b) non-scent breeds, (c) sight breeds (Parker et al., 2017; vonHoldt et al., 2010), (d) ancient breeds (Freedman, Lohmueller, & Wayne, 2016; Parker et al., 2017; Parker, Kim, & Sutter, 2004; vonHoldt et al., 2010), and (e) non-ancient breeds (Table 1). Within this classification, the scent breeds are divided into two subgroups: genetically defined scent breeds, that is, those that have been defined as a monophyletic clade in molecular studies (Arkansas coonhound, basset hound, beagle, bloodhound, dachshund, and English foxhound; see trees in Parker et al., 2017; vonHoldt et al., 2010) and detection dogs, that is, breeds outside that clade that are commonly chosen for scent detection work (German shepherd, German short-haired pointer, golden retriever, and Labrador; Ensminger, 2011; Rocznik et al., 2015). Second, to test whether significant morphological differences in RelCP size exist among any of the functional breed groupings, we classified the domestic dog sample according to overall breed groupings traditionally assigned by breeders (American Kennel Club, 2006; Wilcox & Walkowicz, 1989) (Table 1).

2.3 | Morphological data collection

All specimen skulls were scanned on high-resolution industrial computed tomography (CT) scanners (Phoenix v|tome|x l S; North Star Imaging ACTIS; XRadia MicroXCT;

TABLE 1 Specimen table: study specimens, morphological data, and dog breed groupings

Species	Breed	Specimen ID	Sex	OOL	CPSA	Wild, domestic	Scent, sight	Ancient, non-ancient	Overall breed grouping
Canis familiaris	Airedale terrier	CAS-MAM-26489	M	90.71	489.41	Domestic	Non-scent, non-sight	Non-ancient	Terrier
	American pit bull terrier	PSU239032	M	109.26	643.86	Domestic	Non-scent, non-sight	Non-ancient	Terrier
	American pit bull terrier	PSU234341	U	106.05	584.23	Domestic	Non-scent, non-sight	Non-ancient	Terrier
	American pit bull terrier	PSU238703	F	105.04	604.76	Domestic	Non-scent, non-sight	Non-ancient	Terrier
	American pit bull terrier	PSU239770	M	108.20	628.50	Domestic	Non-scent, non-sight	Non-ancient	Terrier
	Anacapa mix	UCLA2858	U	91.59	499.92	Domestic	Non-scent, non-sight	Non-ancient	Mixed breed
	Arkansas coonhound	YPM004936	M	115.75	767.90	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Basenji	CAS-MAM-26504	F	86.50	420.30	Domestic	Non-scent, non-sight	Ancient	Ancient
	Basset hound	CAS-MAM-26679	M	111.45	773.41	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Basset hound	YPM004943	M	110.56	690.00	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Beagle	UL1	M	93.29	566.19	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Beagle	UL2	M	100.70	524.07	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Beagle	UL3	F	98.37	577.81	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Beagle	UL4	U	98.66	604.26	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Bloodhound	YPM004949	M	133.08	752.56	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Bloodhound	YPM009618	F	121.77	748.71	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Borzoi	CAS-MAM-26481	F	125.32	675.66	Domestic	Sight breed	Non-ancient	Sight hound
	Boston terrier	CAS-MAM-26499	F	78.69	391.79	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Boston terrier	CAS-MAM-32242	M	73.30	368.29	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Boxer	PSU238342	M	101.01	557.22	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Boxer	CAS-MAM-32240	F	93.28	446.54	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Boxer	CAS-MAM-26494	F	104.90	514.03	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Cavalier King Charles spaniel	PSU202840	U	88.22	411.90	Domestic	Non-scent, non-sight	Non-ancient	Spaniel
	Chihuahua	CAS-MAM-33865	U	53.53	213.88	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Chihuahua	CAS-MAM-26681	F	61.84	269.59	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Chowchow	CAS-MAM-26735	U	102.94	565.73	Domestic	Non-scent, non-sight	Ancient	Ancient
	Chowchow	YPM007676	F	98.29	487.01	Domestic	Non-scent, non-sight	Ancient	Ancient
	Cocker spaniel	CAS-MAM-26678	M	92.00	531.39	Domestic	Non-scent, non-sight	Non-ancient	Spaniel
	Cocker spaniel	CAS-MAM-32237	M	98.00	520.18	Domestic	Non-scent, non-sight	Non-ancient	Spaniel
	Collie	CAS-MAM-32244	F	111.60	665.42	Domestic	Non-scent, non-sight	Non-ancient	Herding
	Collie	CAS-MAM-26485	M	122.70	694.30	Domestic	Non-scent, non-sight	Non-ancient	Herding
	Dachshund	CAS-MAM-26680	F	84.55	553.66	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Dachshund	CAS-MAM-33861	U	86.60	530.39	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Dachshund	CAS-MAM-33863	U	79.80	369.43	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	Dingo	CAS-MAM-20735	M	115.05	800.62	Domestic	Non-scent, non-sight	Ancient	Ancient
	Dingo	MVZ119677	M	107.20	604.62	Domestic	Non-scent, non-sight	Ancient	Ancient
	Doberman pinscher	CAS-MAM-26482	M	120.07	651.58	Domestic	Non-scent, non-sight	Non-ancient	Working dog
	English bulldog	CAS-MAM-32241	M	91.20	608.09	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	English bulldog	CAS-MAM-26505	F	104.80	730.22	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	English foxhound	YPM008002	M	133.54	794.81	Domestic	Scent (genetic grp.)	Non-ancient	Scent hound
	French bulldog	UCLA3054	U	81.23	446.28	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like

(Continues)

TABLE 1 (Continued)

Species	Breed	Specimen ID	Sex	OOL	CPSA	Wild, domestic	Scent, sight	Ancient, non-ancient	Overall breed grouping
	German shepherd	PSU233738	M	124.23	823.80	Domestic	Scent (detection dog)	Non-ancient	Working dog
	German shepherd	PSU239103	F	102.83	753.89	Domestic	Scent (detection dog)	Non-ancient	Working dog
	German shepherd	PSU241353	M	117.47	785.82	Domestic	Scent (detection dog)	Non-ancient	Working dog
	German short hair pointer	CAS-MAM-33862	U	110.13	701.99	Domestic	Scent (detection dog)	Non-ancient	Spaniel
	German short hair pointer	CAS-MAM-26677	M	111.40	741.03	Domestic	Scent (detection dog)	Non-ancient	Spaniel
	Golden retriever	PSU238986	M	124.86	632.35	Domestic	Scent (detection dog)	Non-ancient	Retriever
	Golden retriever	PSU239071	M	121.21	700.42	Domestic	Scent (detection dog)	Non-ancient	Retriever
	Golden retriever	PSU241409	F	117.26	731.97	Domestic	Scent (detection dog)	Non-ancient	Retriever
	Great Dane	YPM007251	M	154.44	913.34	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Greyhound	CAS-MAM-26491	M	113.12	664.13	Domestic	Sight breed	Non-ancient	Sight hound
	Irish setter	CAS-MAM-26483	M	107.16	669.33	Domestic	Non-scent, non-sight	Non-ancient	Retriever
	Labrador retriever	PSU239514	U	114.53	618.57	Domestic	Scent (detection dog)	Non-ancient	Retriever
	Labrador retriever	PSU220785	F	117.68	599.06	Domestic	Scent (detection dog)	Non-ancient	Retriever
	Labrador retriever	PSU239622	M	120.41	673.77	Domestic	Scent (detection dog)	Non-ancient	Retriever
	Mastiff	YPM004933	M	144.29	888.37	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Mastiff	YPM004924	M	154.35	892.00	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Miniature pinscher	MVZ135024	F	70.72	289.93	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Pekingese	YPM004945	U	59.19	233.33	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Pekingese	YPM008731	U	64.58	240.08	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Pomeranian	PSU234487	U	75.61	307.30	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Pomeranian	CAS-MAM-26496	F	68.73	282.02	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Pomeranian	CAS-MAM-33864	U	54.49	236.70	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Pug	PSU238770	M	62.79	292.84	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Pug	CAS-MAM-26495	F	70.13	339.75	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Pug	CAS-MAM-32234	M	65.54	260.55	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Rottweiler	CAS-MAM-30704	M	122.65	661.56	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Rough collie	YPM004952	M	113.91	721.55	Domestic	Non-scent, non-sight	Non-ancient	Herding
	Saluki	LACM22825	U	102.34	601.60	Domestic	Non-scent, non-sight	Ancient	Ancient
	Saluki	YPM007471	F	109.44	663.24	Domestic	Non-scent, non-sight	Ancient	Ancient
	Saint Bernard	CAS-MAM-26742	F	129.00	806.10	Domestic	Non-scent, non-sight	Non-ancient	Mastiff-like
	Shar-pei	CAS-MAM-26732	U	111.02	584.98	Domestic	Non-scent, non-sight	Ancient	Ancient
	Shih tzu	CAS-MAM-30873	M	81.82	359.46	Domestic	Non-scent, non-sight	Non-ancient	Toy
	Siberian husky	CAS-MAM-26502	M	117.15	674.23	Domestic	Non-scent, non-sight	Ancient	Ancient
	Swiss mountain dog	PSU180566	M	131.51	873.54	Domestic	Non-scent, non-sight	Non-ancient	Working dog
	Standard poodle	CAS-MAM-26480	M	112.69	783.01	Domestic	Non-scent, non-sight	Non-ancient	Working dog
	Toy poodle	CAS-MAM-26479	M	65.40	293.56	Domestic	Non-scent, non-sight	Non-ancient	Working dog
	Toy poodle	CAS-MAM-32236	F	73.70	387.13	Domestic	Non-scent, non-sight	Non-ancient	Working dog
	Yorkshire terrier	PSU235765	U	68.06	338.29	Domestic	Non-scent, non-sight	Non-ancient	Terrier
	Irish wolfhound	LACM30539	M	125.04	851.57	Domestic	Sight breed	Non-ancient	Sight hound

TABLE 1 (Continued)

Species	Breed	Specimen ID	Sex	OOL	CPSA	Wild, domestic	Scent, sight	Ancient, non-ancient	Overall breed grouping
Canis lupus	Wolf	USNM98311	F	120.78	945.19	Wild	NA	NA	NA
		USNM98307	M	122.43	903.80	Wild	NA	NA	NA
		USNM507338	F	122.37	881.27	Wild	NA	NA	NA
		USNM291012	M	127.02	930.09	Wild	NA	NA	NA
		LACM23010	U	133.10	1,094.47	Wild	NA	NA	NA
Canis latrans	Coyote	UCLA1225	F	95.63	692.36	Wild	NA	NA	NA
		UCLA2739	M	101.37	763.06	Wild	NA	NA	NA
High resolution CT scanners									
Nikon Metrology XT H 225 ST						Molecular Imaging Center, Univ. of South California			
GE Phoenix v|tomex S						General Electric Inspections Technology, San Carlos, California			
North Star Imaging ACTIS						The Univ. of Texas High-Resolution X-ray Computed Tomography Facility			
Xradia microXCT						The Univ. of Texas High-Resolution X-ray Computed Tomography Facility			
Yxlon ff20						California Academy of Sciences, San Francisco, CA			
Imaging software									
Mimics v. 15.0-21.0									Materialise; Leuven, Belgium
3-Matics v. 7.0.1-9.0									Materialise; Leuven, Belgium

Abbreviations: CPSA, cribriform plate surface area; F, female; M, male; Scent (genetic grp.), scent dogs grouped by phylogeny; Scent (detection dog), breeds typically chosen as working detection dogs; OOL, occiput-orbit length; U, unknown sex. Museums and collections: CAS, California Academy of Sciences, San Francisco; UL, Universität Leipzig; LACM, Museum of Natural History Los Angeles County; MVZ, Museum of Vertebrate Zoology, UC Berkeley; PSU, Pennsylvania State University; USNM, National Museum of Natural History; UCLA, Donald R. Dickey Collection; YPM, Yale Peabody Museum.

Nikon Metrology XT H 225 ST). The targeted region of interest was constrained to the CP and the area directly surrounding it in order to increase scan resolution. Scan voxel size ranged from 0.04 to 0.085 mm. All scan data are available through MorphoSource (https://www.morphosource.org/) or Digimorph (http://www.digimorph.org).

To visualize and quantify CP morphology, we imported CT scan data into the 3D imaging software Mimics (v. 20.0-21.0, Materialise Leuven, Belgium), segmented the CP into masks that delineate bone and non-bone, and finally reconstructed 3D volumetric models (Figures 1 and 2). CP surface area is defined here to include only the area of bone perforated by foramina that carried olfactory nerves crossing to the brain. This excludes the lateral flanks of the CP perforated by the ethmoid foramen, a distinctly large passageway for the nasociliary branch of the trigeminal nerve that has no olfactory function. We quantified CP surface area first by rendering the perforated area into a continuous surface area in the imaging program 3-matic (v. 11.0-13.0, Materialise) with a wrapping function that fills all foramina in the CP model and then digitally incising the CP surface along the perimeter of the perforated region (Figure 1d). We digitally calculated the surface area in 3-matic.

2.4 | Statistical analysis

Because CP area increases with body size, we calculated a metric of size-adjusted RelCP size. RelCP was estimated by the residuals from an ordinary least squares regression of $\log_{10}$ values of absolute CP surface area against a body size proxy for all breeds and the two wild canid species. As a body size proxy, we used the distance between the occipital condyles and the anterior extent of the orbit (OOL), a cranial metric shown to correlate with body mass in carnivorans ($y = 2.3x - 3.37$) (Van Valkenburgh, 1990). See Figure 2 for OOL boundaries in the wolf and bloodhound. We chose OOL over total skull length or body mass as a size proxy for two reasons. First, OOL excludes snout length and avoids the confounding effects of large variation in snout length (brachycephaly and dolichocephaly) present in our sample of dog breeds (Schoenebeck et al., 2012). Second, weight was not available in collectors' notes for most specimens, and weights reported by the American Kennel Club are based on breed averages and display large ranges (Crowley & Adelman, 1998). Size-adjusted CP size (RelCP) for each breed or species was estimated as the residuals from a generalized least squares regression of $\log_{10}$ mean values of absolute CP surface area against $\log_{10}$ OOL (Figure 3a,b). Phylogenetic comparative methods were not used here to account for the effects of phylogeny on CP morphology, as existing cladograms for wolves and domestic dog breeds are not time-calibrated due to extensive admixture between breed lineages (Parker et al., 2017).

To test for significant differences in RelCP between wild canids and domestic dogs and between dog breed groupings, we performed pair-wise *t* tests and one-way analysis of variance (ANOVA). Additionally, while testing for differences in RelCP between groupings in various subsets of the data (see Table 2), we performed analysis of covariance (ANCOVA), as it is robust to violations of normality. We carried out all analyses in R (v. 3.5.3) (R Core Team, 2014).

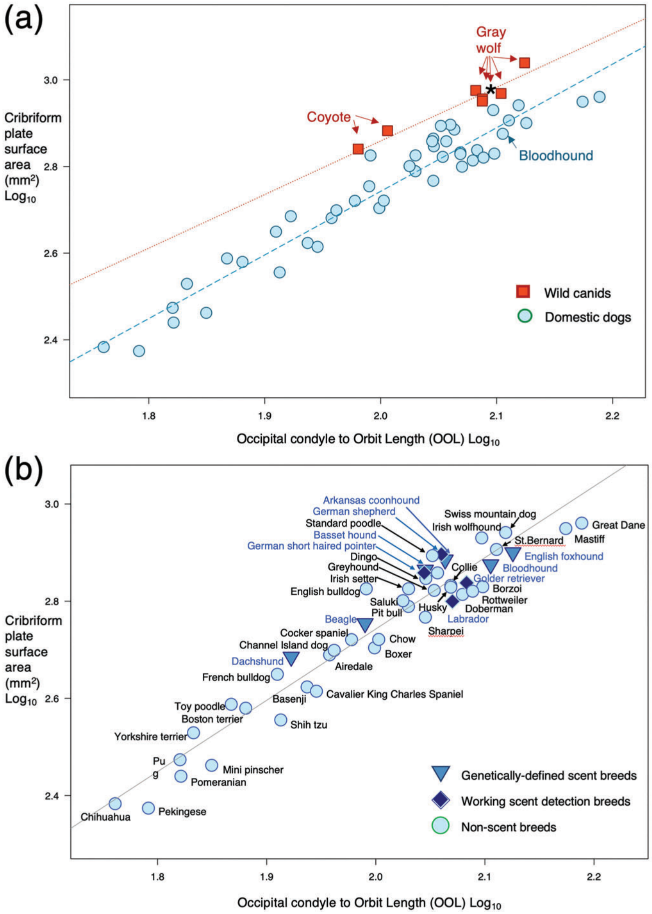

FIGURE 3 Cribriform plate morphology in domestic dog breeds and their closest wild canid relatives, the gray wolf and coyote. Log–log plot of CP surface area versus body size metric, occiput to orbit length (OOL). (a) Domestic dogs have on average significantly smaller relative CP than wolves alone as well as wolves grouped with coyotes ($p < .001$). Regression equation: $y = 1.52x - 0.285$. See Figure 2 for comparison of CP morphology in wolf (asterisk above) and bloodhound. (b) Within species comparison of RelCP shows no significant difference between non-scent breeds and scent breeds, defined here as either a monophyletic group (inverted triangles) or working detection dogs (dark blue diamonds). Regression equation: $y = 1.449x - 0.158$

3 | RESULTS

To examine the scaling relationship between CP morphology and body size, we plotted CP surface area against our body size metric, OOL, using log–log generalized least square regression. Across our canid sample of 45 domestic dog breeds, one mixed breed and the wolf and coyote, CP surface area scales to body size with negative allometry ($r^2 = .89$, $p < .001$, $y = 1.52x - 0.285$) (Figure 3a and Table 2). The slope is significantly lower than what is expected under geometric similarity (slope of 2) and indicates that larger canids have relatively smaller CP for their size.

To test our hypothesis that the domestic dog has undergone reductions in olfactory anatomy at some point after its evolutionary split from the wolf, we compared the RelCP, or residuals from a log–log regression of CP surface area versus the body size proxy OOL, in dogs and the two closest canid relatives, the gray wolf and the coyote. Domestic dogs have on average a significantly smaller RelCP than the wolf alone as well as the wolf and coyote combined (Figures 3a and 4a and Table 2). A notable exception is the English bulldog, which has a RelCP larger than three of the wild canids (Figure 3b). The one dog in our sample without a breed assignment, the California Channel Islands dog, fits among the defined breed dogs, in that it has a comparably small CP relative to the wild canids (Figure 3b).

Given that previous studies found evidence of admixture with wolves particularly among "ancient" domestic dog breeds (Freedman et al., 2014; vonHoldt et al., 2010), we tested whether "ancient" breeds in our sample ($n = 6$, dingo, basenji, Siberian husky, chow chow, saluki, sharpei) have retained olfactory anatomy closer in size to that of the wolf than the other domestic dogs. A pair-wise *t*-test and ANCOVA show there is no difference between RelCP size in "ancient" breeds and that of all other domestic dog breeds ($p = .6$; Figure 4c and Table 2). By contrast, there is a significant difference between the RelCP of the six "ancient" breeds and that of the wild canids, the wolf and coyote, as well as between "ancient" breeds and wolves alone ($p < .001$; Table 2). In both cases, relative to the wild canids, the ancient breeds have smaller RelCP.

Within the domestic dogs, scent breeds do not have a more robust olfactory anatomy than non-scent breeds, based on RelCP values estimated from a log–log regression of CP surface area versus OOL in domestic dogs alone. The olfactory anatomy of scent hounds (genetically defined scent hounds, $n = 6$) is on average no larger than that of non-scent breeds ($p = .57$; Figure 4b and Table 2). Adding scent detection breeds ($n = 4$) to the scent breed grouping does not change the situation; there is still no significant difference between scent and non-scent RelCP ($p = .14$; Figures 4b and 5; Table 2). A narrowed comparison between the RelCP in scent breeds ($n = 10$) and sight breeds alone ($n = 3$) again shows no significant difference in RelCP (Figure 5, sight breeds noted by red stars). By contrast, scent breeds ($n = 10$) have significantly smaller RelCP than the wild canids in our sample, the gray wolf and coyote ($p < .001$; Table 2).

It is beyond the scope of this article to perform a quantitative analysis of the influence of relative snout length on CP size across our sample, and we save this for a future study. However, we can report that based on cephalic indices assigned to breeds in a previous study (Schoenebeck et al., 2012), breeds with the shortest faces in our sample have among the smallest and largest RelCP (see Pekingese, shih tzu, rottweiler, English bulldog in Figure 5).

A pairwise comparison of RelCP variation across conventional dog breed groupings defined by the American Kennel Club and the *Atlas of Dog Breeds of the World* (American Kennel Club, 2006; vonHoldt et al., 2010; Wilcox & Walkowicz, 1989) revealed that, within the species *Canis familiaris*, there is no significant difference in olfactory anatomy between any of the breed groupings (Table 2). No breed grouping stands out as having either unusually large or small olfactory morphology. For example, the "mastiff-like" grouping itself includes breeds covering a wide range of RelCP, from the short-snouted English bulldog with the largest RelCP to the Great Dane with the fourth smallest RelCP (Figure 5).

4 | DISCUSSION

In the course of its domestication from the gray wolf, it appears that the dog has lost some of its olfactory capacity. We found a significant reduction in olfactory anatomy, specifically the surface area of the CP relative to body size (RelCP), across domestic dog breeds compared with the gray wolf and the coyote. This supports previous anatomical work documenting varying degrees of olfactory loss, coupled with overall brain size reduction, in association with domestication in the rat, sheep, llama, and one dog breed (Kruska, 1988). Likewise, Güntherschulze (1979) estimated a lower number of olfactory sensory neurons in the nasal epithelium of the domestic pig (*Sus scrofa domesticus*) than that of the European wild boar (*Sus scrofa scrofa*). Based on these previous studies, we might assume that our finding of olfactory loss in the domestic dog conforms to a generalizable pattern of olfactory loss in all domesticated mammals. However, evidence from a recent molecular study revealed contrary results in the Tibetan wild boar and domestic Duroc pig, in which there was an expansion of the OR gene repertoire (~1,240 genes) in the pig relative to the wild boar (~752) (Li, Shilin, Long, Guangyu, et al., 2013). Because it is known that CP size correlates closely with OR gene repertoire size across a wide array of mammal species (Bird et al., 2018), a larger OR gene repertoire here may indicate that the domestic Duroc pig has a comparable, perhaps larger, olfactory apparatus than its wild counterpart.

Given that the pig data suggest that domestication might not always result in olfactory loss, why do we see an apparent decline in olfactory capacity in the domestic dog relative to its ancestor, the gray wolf? We might infer from this decline that selection for enhanced olfactory abilities is relaxed in dogs relative to wolves. This likely occurred over time as dogs or proto-dogs became increasingly reliant on food supplied by humans. Released from the need to actively hunt, the dogs would no longer require the heightened olfactory capacity required for accurate long-distant detection and tracking of prey (Gittleman, 1991; Smith, 1980). Additionally, relaxed purifying selection may have led to an increased frequency of deleterious genetic variants in olfactory-related genes due to several population bottlenecks during the initial wolf-dog divergence as well as much later during the development of domestic dog breeds over the last several hundred years (Cruz, Vila, & Webster, 2005; Freedman et al., 2014; Wayne & Ostrander, 2007).

It is unclear at this point whether the decline in RelCP is coupled with a decrease in brain volume in the domestic dog relative to the wolf. As noted above, decreased brain weight is associated with domestication in several mammal species but not all (Kruska, 1980, 1988, 2005). In his study comparing brain size in domestic mammals with their wild counterparts, Kruska (1980) found that in domestic rats, sheep, pigs, and one breed of dog (poodle) reductions in olfactory brain structures (olfactory bulb and tuberculum, piriformis, etc.) were in nearly direct proportion to losses in overall brain capacity. In future work, we need to investigate our sample of wolves, coyotes, and 45 dog breeds to determine first whether domestic dogs' brain size is on average reduced relative to wild canid relatives and second, if CP reduction in domestic dogs covaries with, or is independent of, brain size fluctuations.

The reduction in the olfactory skeleton seen in the domestic dog relative to the wolf is common to all breed groups, including both the "ancient" breed and scent breed groups. Because "ancient" breeds originated over

TABLE 2 Summary statistics

Regression	*N* (species, breeds)	r^2	*p* value	Regression equation
CP surface area vs. OOL (body size proxy)				
Dog breeds, coyotes and gray wolves	52	.89	<.001	$y = 1.52x - 0.285$
Dog breeds only	45	.92	<.001	$y = 1.449x - 0.158$
Coyotes and gray wolves only	7	.92	.003	$y = 1.237x + 0.3845$
Scent and sight breeds only	13	.68	<.001	$y = 1.03x + 0.7295$

		Pairwise *t* test		ANCOVA	
	N	*p* value	Bonferroni corrected *p* value	F	*p* value
Domestic dogs vs. wild canids					
RelCP; all dogs vs. gray wolf and coyote	53	<.0001	<.0001	34.54	<.0001
RelCP; all dogs vs. gray wolf alone	51	<.0001	<.0001	40.18	<.0001
RelCP; “ancient” breeds vs. gray wolf and coyote	13	<.0001	<.0001	48.28	<.0001
RelCP; “ancient” breeds vs. gray wolf	11	<.0001	.002	14.16	<.0001
RelCP; scent breeds vs. gray wolf and coyote	17	.0006	.005	24.38	<.0001
Dogs; breed groupings					
RelCP; “ancient” breeds vs. non-ancient breeds	46	.6	NS	0.63	.43
RelCP; scent breeds (genetically defined, $n = 6$ plus detection dogs, $n = 4$) vs. all non-scent breeds	46	.13	NS	2.48	.12
RelCP; genetically defined scent hounds ($n = 6$) vs. all non-scent breeds	46	.16	NS	1.77	.19
RelCP; scent breeds ($n = 10$) vs. sight breeds ($n = 3$)	13	.48	NS	0.04	.84

One-way ANOVA			
	N	F	*p* value
RelCP; all breed groupings, as assigned by breeders and American Kennel Club (no. groups = 10) (see Table 1)	45	$F_{9,36} = 1.48$	.23

Abbreviations: ANOVA, analysis of variance; ANCOVA, analysis of covariance; CP, cribriform plate; OOL, occiput to orbit length; RelCP, relative cribriform plate size.

500 years ago and have experienced intermittent admixture with wolves (American Kennel Club, 2006; Freedman et al., 2014; Parker et al., 2017; vonHoldt et al., 2010; Wilcox & Walkowicz, 1989), we reasoned that “ancients” might retain a partial ancestral state in the form of a more robust olfactory morphology. However, we found no significant difference between the CP morphology of the six “ancient” breeds in our sample (dingo, basenji, chow chow, Siberian husky, saluki, and shar-pei) and that of the 39 other “modern” dog breeds and one mixed breed dog. As was true of the modern breeds, the “ancients” had a reduced RelCP relative to the wild canids (Table 2). Consequently, the relative olfactory capacity and CP size of “ancient” dog breeds appear to be more shaped by early domestication and later artificial breed selection than historical admixture with wolves.

Surprisingly, despite their legendary status as “super sniffers,” scent breeds do not have the olfactory anatomy to back up their moniker. Genetically related scent breeds (Arkansas coonhound, basset hound, beagle, bloodhound, dachshund, English foxhound) as well as breeds commonly employed in scent detection work (German shepherd, German short-haired pointer, golden retriever, Labrador) have CPs that are on average no more robust than those of sight hounds (borzoi, greyhound, Irish wolfhound) or those of all the non-scent breeds combined. Even the bloodhound, described on a breeder website as “a nose with a dog attached” and attributed with an unreferenced number of olfactory sensory neurons three times that of any other breed (https://wychwaybloodhounds.com/home), had a small RelCP among the scent breed grouping (Figure 5). Indeed, the average RelCP of scent hounds ($n = 10$) stands out only

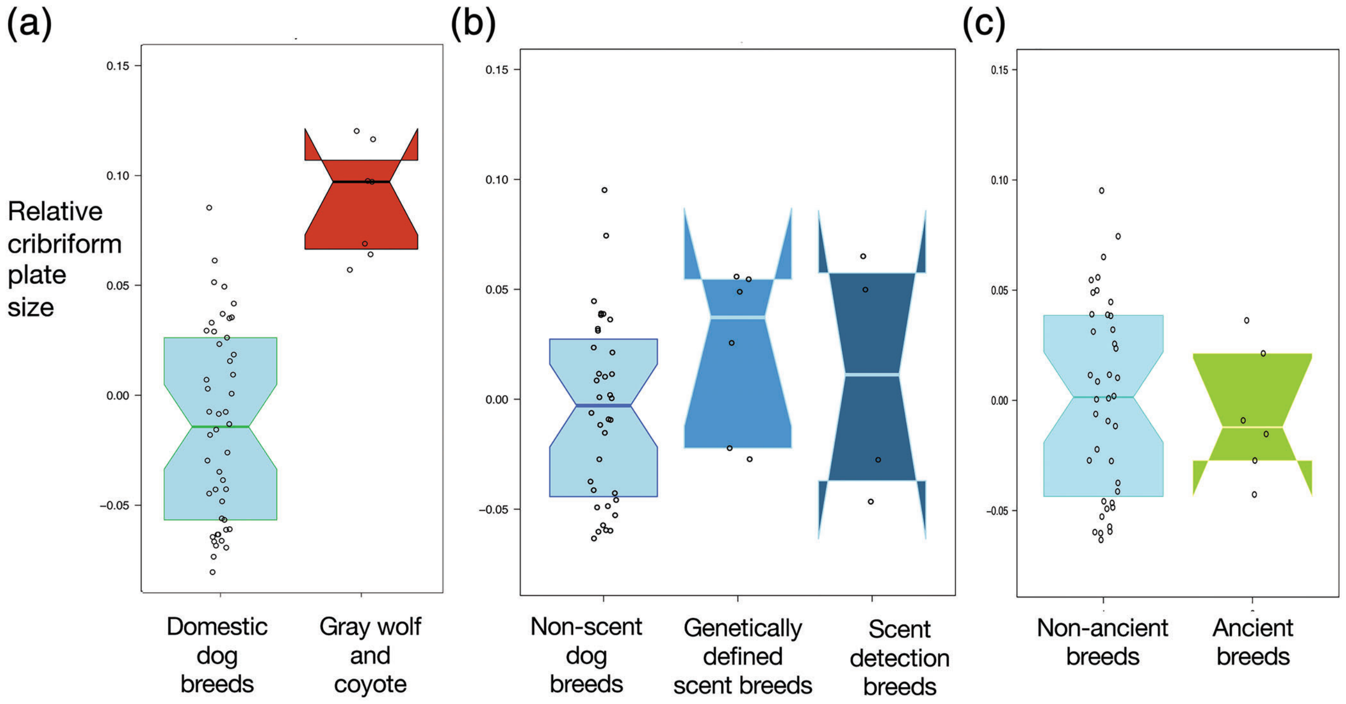

FIGURE 4 Notched boxplots for comparisons of relative CP size in canid groupings. (a) Domestic dog breeds versus gray wolves and coyotes ($p < .001$). An outlier among the domestic dogs, the English bulldog, overlaps with the wild canids. (b) Among domestic dog breeds, non-scent breeds versus scent breeds (NS). (c) Among domestic dogs, non-ancient versus ancient breeds (NS)

in its being significantly smaller than that of the wolf and coyote, as well as the wolf alone ($p < .001$; Table 2). Repeated historical claims that scent dogs were bred for a good nose, a trait suitable for the emerging foxhunting pastime (Crowley & Adelman, 1998) suggest that olfactory strength was directly selected for in the early development of scent breeds. On the contrary, we found no clear evidence in the scent breeds' CP morphology that artificial selection retained or recovered the ancestral, wolf-like olfactory condition, supporting the hypothesis that scent breeds are scent breeds in name only.

Nevertheless, a recent behavioral study on dogs found that six breeds defined as having been selected for scent work outperformed 17 other breeds in scent detection tests (Polgár, Kinnunen, Újváry, Miklósi, & Gácsi, 2016). It is difficult to compare this study with ours. First, only three of their scent breeds were included in our list of 10 scent breeds, reflecting the fact that defining breeds selected for olfactory ability is somewhat arbitrary and subject to regional variation. Second, prior training can confound comparisons of dogs' olfactory abilities. Although the behavioral test was designed by Polgar et al. to avoid the training required in most scent detection or discrimination tests (Johnen, Heuwieser, & Fischer-Tenhagen, 2013; Walker et al., 2006), three of the six scent breeds chosen for this study had prior training in human trailing. Given that we found no evidence for any anatomical advantage in the nose of scent dogs, we suggest that scent detection dogs might be chosen not so much for olfactory prowess but specifically for behavioral traits that make them more trainable. Indeed, when dog handlers with the United States Transportation Security Administration were asked to list favorable traits in successful detection dogs, their top ranked traits included calmness, concentration, human-perceived relationship, playfulness, search drive, alertness, and human focus. Use of olfaction ("sniffing") was given far less priority (Rocznik et al., 2015). In the same vein, the AKC detection dog task force actively recruits Labrador retrievers and German short-haired pointers because of their putative attributes of strong hunting drives, reliable temperaments in public settings and high energy (https://www.akc.org/akc-detection-dog-task-force/akc-pilot-detection-puppy-rearing-program/).

Although our anatomical data suggest that there has not been directed artificial selection for dogs with increased olfactory capacity, further tests are needed to rule this out. For example, nasal turbinal architecture and fluid dynamics in nasal airflow and odorant deposition patterns might differ between scent and non-scent breeds (Craven, Paterson, & Settles, 2009; Van Valkenburgh et al., 2014). In addition, the number of OR genes found in scent dogs' genomes should be compared to those of both non-scent breeds and wolves, as the size

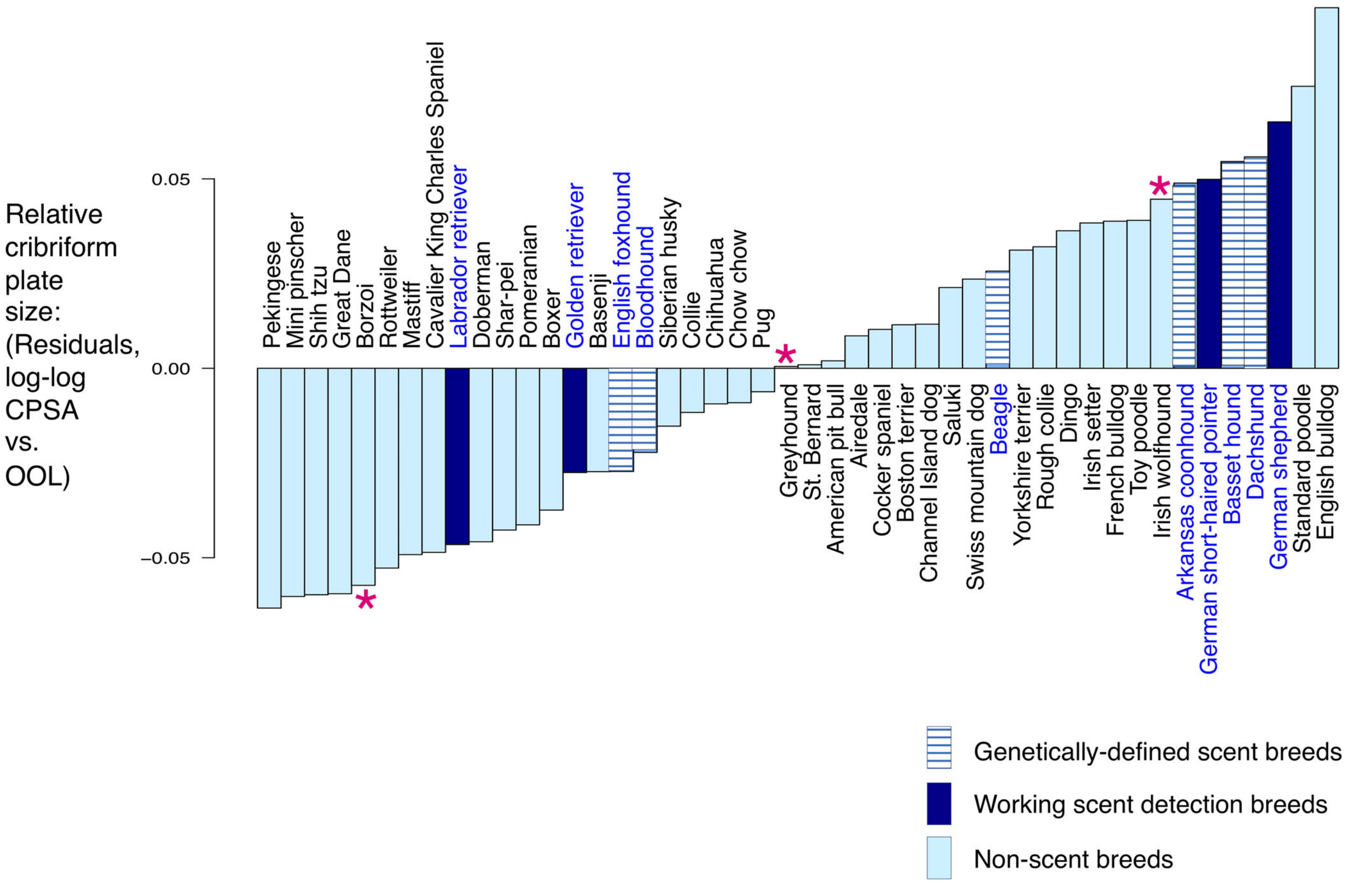

FIGURE 5 Simple rank order of residuals from Figure 3b, (relative CP size), in scent and non-scent breeds. Scent breeds (dark blue and blue striped bars) have no larger relative CP than sight breeds in particular (red asterisk) as well as all non-scent breeds. See Table 2

of the OR gene repertoire has been shown to correspond with the ability to discriminate odorants and correlates closely with olfactory morphology across species (Bird et al., 2018; Rizvanovic, Amundin, & Laska, 2013).

Finally, our finding that the brachycephalic English bulldog has the largest RelCP among the domestic dogs in our sample was surprising, given that short-snouted dogs are generally assumed to lack the nasal space for a sizable olfactory system and are not chosen by detection dog handlers (Jamieson, Baxter, & Murray, 2017; Jones, Dashfield, Downend, & Otto, 2004). Aside from the English bulldog, most of the short-nosed dogs in our sample (e.g., Pekingese, shih tzu, rottweiler, mastiff) are at the other side of the spectrum, possessing some of the smallest CP for their body size (Figure 5). Little is known about the influence of snout length on relative olfactory capacity in dogs. Much has been written about respiratory anatomy and associated pathologies in brachycephalic dogs (Schuenemann & Oechtering, 2014) but less about olfactory anatomy. A current study revealed that CP shape in dogs tends to follow differences in external skull morphology and that the CP in short-faced breeds is generally flattened in the rostral–caudal orientation relative to other breeds (Jacquemetton, Drexler, Kellerman, Bird, Van Valkenburgh, 2020); however, it is yet unclear whether CP shape plays any functional role in olfactory performance. Few scent detection trials include brachycephalic dogs, and in one such study the performance by short-snouted dogs was mixed: it was poor compared with scent breeds but no different from non-scent breeds (Polgár et al., 2016). Our data indicate that possession of a short snout in a breed does not necessarily result in a diminished CP and therefore might not negatively affect olfactory capacity. It is notable here that short snouts can be relatively narrow as in the mastiff, or wide as in the English bulldog; thus, it may be the overall volume of the snout that determines CP size. Future work will focus on quantifying snout dimensions in more detail to determine potential constraints on the development of the olfactory skeleton.

The pattern of RelCP loss in the dog relative to its ancestor the wolf found in this study is consistent with a prior study showing reductions in olfactory-related brain structures associated with domestication in some species (Kruska, 1988). However, the more surprising and notable finding of this study is that RelCP loss in the domestic dog is consistent across all dog breed groupings and, with the exception perhaps of the English bulldog, across all individual dog breeds. While our results should be further tested against corresponding olfactory data, such as OR gene repertoires (Bird et al., 2018), ethmoid turbinal surface area, or olfactory epithelium area (Van Valkenburgh et al., 2014; Yee, Craven, Wysocki, & Van Valkenburgh, 2016), current findings suggest a decrease in the olfactory anatomy at some point in the history of dogs and a lack of restoration of CP size in any of the dog breed groupings, even those attributed with sniffing super powers and purportedly bred for a keen sense of smell. It is not yet possible to know whether the size of the CP decreased in dogs as a result of initial domestication or subsequent breed selection; however, using the methods described here to quantify CP dimensions in ancient and historical specimens of dogs could bring us closer to understanding this.

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AUTHOR CONTRIBUTIONS

Deborah J. Bird: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; visualization; writing-original draft; writing-review and editing. **Sophie A. Buelow:** Data curation; investigation; writing-review and editing. **Andrew W. Evans:** Data curation; investigation; writing-review and editing. **Blaire Van Valkenburgh:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; writing-review and editing.

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