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Research

Brain size reduction in dogs was already established at least by the Late Neolithic of Western Europe, 5000 years ago

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Thomas Cucchi[1], Lucile-Morgane Hays[1], Alessio Veneziano[1], Margot Michaud[2,3], Colline Brassard[4,5], Rose-Marie Arbogast[6], Pierre Pétrequin[7], Mietje B. Germonpré[8], Evelyne Crégut-Bonnoure[9], Frédéric Elleboudt[10,11], Kalman Czeibert[12], László Zsolt Garamszegi[13], Enikő Kubinyi[12], Niclas Kolm[14], Tibor Csörgő[12], Justine Joseph[15], Salomé Leroy[15], Claude Guintard[15], Marion Fusellier[15], Christophe Duchamp[16], Anthony Herrel[4,17,18,19], Loukas George Koungoulos[20,21], Thomas J. Peachey[21], Lachie Scarsbrook[22,23], Laurent Frantz[22], Joan Madurell-Malapeira[24] and Sandrine Ladevèze[25]

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[1]UMR 7209 'BioArch—BioArchéologie, Interactions Sociétés environnements', Muséum national d'Histoire naturelle, Paris, France
[2]Institut Polytechnique UniLaSalle, IDEALISS ULR 7519, Universite d'Artois, France
[3]Evolution and Diversity Dynamics Lab, University of Liège, Liège, Belgium
[4]Mécanismes Adaptatifs et Evolution, UMR 7179, Muséum national d'Histoire naturelle CNRS, Paris, France
[5]VetAgro Sup, Campus vétérinaire de Lyon, Marcy-l'Étoile, France
[6]UMR 7044 ArcHiMèdE, Misha 5 allée du Général Rouvillois 67083 Strasbourg Cedex, France
[7]MSHE Ledoux, CNRS and Université de Bourgogne-Franche-Comté, Besançon, France
[8]Earth and History of Life, Royal Belgian Institute of Natural Sciences, Brussels, Belgium
[9]TRACES, UMR 5608, CNRS université Toulouse Jean Jaurès, Toulouse, France
[10]INRAE, CNRS, Université de Tours, PRC, 37380, Nouzilly, France
[11]INRAE, Université de Tours, CHU de Tours, PIXANIM, 37380, Nouzilly, France
[12]Department of Ethology, Institute of Biology, ELTE Eötvös Loránd University, Budapest, Hungary
[13]HUN-REN Centre for Ecological Research, Budapest, Hungary

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Author for correspondence:
Thomas Cucchi
e-mail: cucchi@mnhn.fr

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[14]Department of Zoology, Stockholm University, Stockholm, Sweden
[15]Nantes-Atlantic National College of Veterinary Medecine, Food Science and Engineering, Oniris-VetAgro Bio, Nantes, France
[16]Office Français de la Biodiversité, Régie Micropolis, Gap, France
[17]Naturhistorisches Museum Bern, Bern, Switzerland
[18]Department of Biology, Evolutionary Morphology of Vertebrates, Ghent University, Ghent, Belgium
[19]Functional Morphology Laboratory, Department of Biology, University of Antwerp, Antwerp, Belgium
[20]School of Social Sciences, University of Western Australia, Australia
[21]Australian Museum Research Institute, Sydney, Australia
[22]Animal Systems Genomics, Faculty of Veterinary Medicine, Ludwig-Maximilians-Universität, Munich, Germany
[23]Palaeogenomics and Bio-Archaeology Research Network, School of Archaeology, University of Oxford, Oxford, UK
[24]Earth Science Department, University of Florence, 50121 Florence, Italy
[25]UMR 7207 Centre de Recherche en Paléontologie, Paris (CR2P), CNRS/MNHN/Sorbonne, France

TC, 0000-0001-6021-5001; MM, 0000-0001-7075-9862; KC, 0000-0001-9425-0892; LZG, 0000-0001-8920-2183;
NK, 0000-0001-5791-336X; TJP, 0000-0001-8557-2363; JM-M, 0000-0003-4639-9451

The timing and causes of brain size reduction in domestic dogs remain uncertain. Using endocast volume as a proxy for brain size, this study provides a first insight into long-term brain size evolution in the wolf-dog lineage. We compared endocranial volumes of 185 modern and 22 prehistoric wolves and dogs ranging from Western Europe to Australia, and spanning the Pleniglacial (35 000 yr BP) to the Late Neolithic (5000 yr BP). Our results reveal that Pleistocene so-called 'protodogs' show no brain size reduction compared with coeval Pleistocene wolves. Instead, we observed a slightly larger relative endocranial volume in the 35 000-year-old 'protodog' from Goyet, which could suggest increased behavioural flexibility in the presence of humans. In contrast, Late Neolithic dogs show a drastic brain size reduction (46%) with endocranial volumes comparable to modern small terrier and toy breeds. We speculate that the anxious and wary temperaments of these Late Neolithic dogs, induced by the brain tissue reorganization associated with such a size reduction, could have served an alerting purpose, among the many other potential roles dogs could have played within these Late Neolithic socio-ecosystems.

1. Introduction

Reduction in brain size is one of the most widely reported biological consequences of domestication [1], often cited as the most reliable marker of the domestication syndrome [2]. Proposed explanations for this decrease include the high energetic costs of the maintenance of neural tissue [3], relaxed selection from predation, foraging, and mating demands, reduced cognitive challenges in the captive environment [4] and behavioural selection [5], with the pleiotropic effects of selection for tameness [6]. Yet, its evolution in the course of the multi-millennial domestication history is still unknown [7].

Among domestic mammals, dogs have had the most pronounced brain size reduction, with an average decrease estimated at 20–30% [8,9]. The current understanding of the dog brain size evolution assumes a two-phase trajectory, with an initial reduction during the wolf-to-dog transition [7], followed by increases in specific brain regions involved in carrying out more complex tasks in the human environment [5]. However, this theory has been made from analysing modern populations, and we know from archaeological and paleogenetic studies that the evolutionary relationship between dogs and humans spans at least the last 20 000 years [10–15]. Some zooarchaeological studies have even suggested that the domestication process could have started as early as 35 000 years ago, with morphometrically divergent specimens described as 'protodogs' [16,17]. Yet, some have argued that this brain size reduction rather reflects very recent breed formation over the last 200 years, when strict aesthetic standards and intensive artificial selection were imposed [10,18]. And finally, neuroscientific studies of modern dogs suggest that recent breeding selection has also increased the cerebral cortex to enhance behavioural flexibility and sensitivity to human social cues [19].

Therefore, to understand the evolution of dogs' brain, the archaeological record is required [20], as well as a modern comparative corpus that covers as much dogs' behavioural diversity as possible, including populations unaffected by recent selective breeding [21,22]. Such populations exist as free-ranging dogs from around the world, including dingoes and village dogs. Dingoes descend from East Asian dogs that were introduced to Australia at least 3300 years ago [23,24] and have since adapted to become Australia's apex terrestrial predator, living largely independent of humans [25]. Village dogs, in turn, are free-ranging populations that live and reproduce with little direct human intervention and represent the vast majority of the global dog population [26].

In this study, we provide the first insight into dog brain size evolution through the analysis of endocast reconstructed from archaeological crania. To do so, we assessed endocranial volume (ECV) from computed tomography (CT) -derived endocasts as a proxy for brain size [9], analysing both absolute ECV and relative ECV (rECV), using cranial measurements to account for body size differences. Because body size can evolve more rapidly than brain size in carnivorans [27], absolute brain size remains an important measure in its own right and may more directly reflect functional performances [28]. Moreover, a recent neuroanatomical study suggests that absolute brain size might bear more information about behaviour and temperament of dogs than relative brain size [29]. Finally, to integrate neurocranial morphology with brain size, we also took linear skull measurements from three-dimensional models of the same specimens and compared them with previously published metrics from modern and ancient canids, thereby capturing the full extent of cranial diversity including those which predate the onset of intensive selective breeding.

The archaeological dataset includes Pleniglacial (>20 000 yr BP) and Post-glacial wolves from Belgium, two so-called 'protodogs', namely a Pleniglacial, approximately 35 000 yr BP specimen from Goyet (Belgium) [16] and a Late Glacial, approximately 15 000 yr BP specimen from Baume Traucade (France) [30]. It also includes a rare assemblage of well-preserved Late Neolithic wolves and dogs from a 5000- to 4500-year-old lakeshore site [31,32]. The modern dataset includes wild wolves and a broad representation of dogs, including dingoes, village dogs and dog breeds covering all functional behaviours selected over the last 250 years [33]. With this dataset, we assessed (i) whether Upper Pleistocene 'protodogs' display neurocranial size differences compared with Pleistocene and Holocene wolves consistent with an early domestication-linked brain size reduction and (ii) whether the transition to the Neolithic farming socio-ecosystem represents an important step in dogs' brain size evolution, and how these changes compare with those observed in modern breeds and free-ranging populations (dingoes and village dogs).

2. Data collection

We collected CT scans from 163 crania of adult modern wolves and dogs from six different institutions (details in electronic supplementary material, table S1), along with 22 crania of prehistoric adult wolves and dogs from Belgium and France (details in electronic supplementary material, table S2). We only CT-scanned the cranium of specimens having their four permanent upper molars in order to exclude juvenile specimens. Thus, all specimens were at least seven months old and sexually mature. CT acquisitions were obtained at different facilities and under varying acquisition parameters (for details, see electronic supplementary material, table S3). We only selected specimens that showed no major damage to the neurocranium, which could compromise the virtual reconstruction of the endocast.

The modern wolf dataset (n = 59) includes 58 wild males and females from France that were shot during a legal control campaign (2020–2022) in southern France performed by the French Biodiversity Office (OFB) or collected after death (either from natural causes or collisions with cars). We also included one 19th-century wolf from the Ardennes region in Belgium. The modern dog dataset (n = 104) includes: (i) 19 village dog skulls from the London Natural History Museum (NHM) that were collected during the nineteenth and twentieth centuries across the world (Russia, Nepal, Chile, Japan, India, Egypt, Sudan, Malaysia, Arabian Peninsula, etc.); (ii) 21 dingoes from the Australian Museum collected from the same region of arid inland Western Australia between 1950–1954 and are thought to represent a single population; and (iii) 64 dogs selected from the Eötvös Loránd University dog skull collection [34] that includes 44 breeds across 17 phylogenetic clades [35] and 7 traditional functions according to the American Kennel Club's (AKC, www.akc.org). These functional groupings are: (i) working, which includes the oldest and largest breeds, selected to assist humans with various working duties such as pulling carts or sledges, guarding and protecting; (ii) toy, which includes the smallest breeds, which are used for companionship; (iii) herding, which includes breeds that are known for their trainability and natural intelligence, and that were developed for moving stock (sheep, cattle and reindeer); (iv) sporting, which includes breeds used to assist during hunting by locating and retrieving feathered game; (v) hound, which includes breeds selected to chase and pursue warm-blooded quarry; (vi) non-sporting, which includes a wide variety of breeds used as watchdogs and house dogs, mainly sought as companion dogs that are good with people; and (vii) terrier, which includes breeds selected for hunting, vermin control and guarding.

The archaeological wolf and dog dataset (*n* = 22; figure 1; details in electronic supplementary material, table S2) included skeletally mature specimens collected from sites in Belgium and France. Specimens from Belgium include two Pleistocene wolves, one Pleniglacial 'protodog' according to skull morphometrics [16], one Postglacial wolf and one Neolithic wolf from Antwerpen [36]. Specimens from France include a recently excavated and studied Late Glacial 'protodog' from France (Baume Traucade) [30]. The five wolves and 10 dogs from the Middle/Late Neolithic lake dwelling site of Chalain were collected among refuse deposits with other animal remains and not as part of a burial [32]. Wolves and dogs are easily distinguishable from linear measurements of skulls and long bones [37]. The dog remains found at Chalain are mainly represented by crania and mandibles [38,39] but also by body ornaments made from canine teeth and metapodials [40], with no obvious butchery marks on the bones, which together suggest a polyvalent use for these dogs [37]. Some articulated dog remains from Chalain have been found inside or outside the village, but of the crania that we could include in this study, all come from refuse areas deposited along with other animals' remains consumed by the people living in this village. The shoulder height of the Chalain dogs, based on long bone measurements, is about 35–45 cm (R. M. Arbobast 2008, unpublished data), and their skull morphology suggests a distant resemblance to modern herding breeds [38].

3. Virtual endocasts and skull measurements

Virtual reconstructions of endocasts (figure 2) from conventional CT were semi-automated from DICOM files using the 'Wrap Solidify' extension for 3D Slicer (freeware, open source; https://www.slicer.org [41]). Their volume in mm^3 (ECV) was then automatically calculated with the 3D Slicer module. Virtual reconstructions of endocasts from µCT were automated using the AST-3D tool introduced in [42]. The AST-3D tool works on a three-dimensional cranial mesh intermediate, which we obtained through isosurface interpolation of the µCT volumes using the function *vcgIsosurface* in the R package *Rvcg* [43].

Measurements (figure 2) were taken from the cranium three-dimensional model using Meshlab [44]. We recorded five measurements: (i) total cranium length (TL), (ii) maximum cranium width (W), (iii) foramen magnum breadth (FMb), (iv) greatest palatal breadth (GPB) and (v) basal cranium length (BL). We then calculated the skull index or cephalic index (CI) as follows: (cranium width / cranium length) × 100. According to their CI, domestic dogs were then categorized into one of the three head groups (dolichocephalic, mesocephalic and brachycephalic) following [9]. TL and CI of modern dog breeds were compiled from multiple published sources [8,45,46]. Among the 59 wolves from France, we measured 12 crania. We also collected TL data for Pleistocene, Mesolithic and Neolithic Eurasian wolves and dogs from the literature (see details in electronic supplementary material, table S4).

4. Statistics

Basic statistics (mean, standard deviation, minimum and maximum) were collected for the ECV and TL (electronic supplementary material, table S5). Since variation among the different functional groups of dogs (AKC), wolves and archaeological wolves and dogs was not homogeneous for ECV (Levene's test: d.f. = 157,18; *F*-value = 2.226 and $p = 0.005$) and rECV (Levene's test: d.f. = 106,14; *F*-value = 2.833 and $p = 0.004$), we compared differences among groups using non-parametric Kruskal–Wallis and Dunn's tests with Bonferroni correction for pairwise comparisons. Differences in variation of TL, ECV and rECV values across groups were visualized with box plots.

To compare ECV and rECV differences across dogs, we grouped them according to their head categories (dolichocephalic, mesocephalic and brachycephalic) following [9], and by their AKC traditional functions. We compared rECV across modern and ancient specimens using linear regression of ECV (dependent) against total cranium length (TL) as the independent variable, including factors distinguishing wolves, dingoes, village dogs and cephalic index categories of dog breeds. To test the difference in rECV variation across modern and ancient specimens, while taking into account the

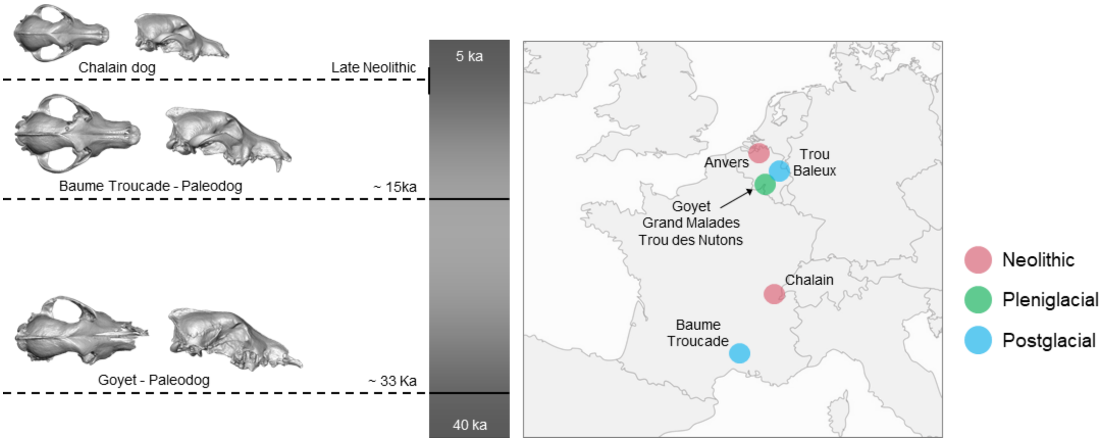

Figure 1. Left: timeline with cranium dorsal and lateral views of the Pleniglacial (Goyet) and Late Glacial (Baume Traucade) 'protodogs' and one Late Neolithic dog of Chalain. Right: map showing the location of the archaeological sites studied.

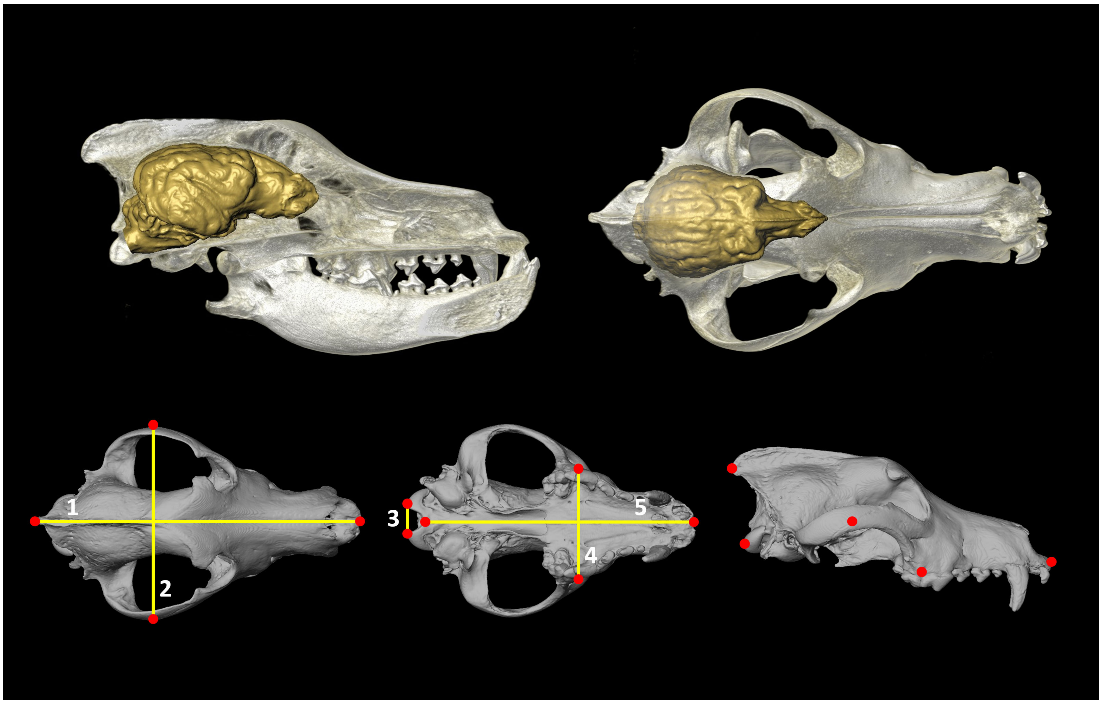

Figure 2. Volume-rendered skull model of a nineteenth-century wolf (RBINS) with the endocast approximating the brain positioned within the braincase, in right lateral view (at the upper right, midsagittal section), and dorsal view (at the upper left). The lower panels from left to right show dorsal, ventral and right lateral views of the wolf cranium with anatomical landmarks for the measurements taken in this study: 1. total cranium length (TL), 2. cranium width, 3. foramen magnum breadth (FMb), 4. greatest palatal breadth (GPB), 5. basal length (BL). Not to scale.

allometric relationship between brain and body sizes, we used the residuals of the linear regression model as rECV values following [9].

All statistical analyses were performed with R v. 4.4.2 [2].

5. Results

5.1. Skull size in modern and ancient dogs and wolves

Ancient and modern wolves and dogs display significant differences in skull length (Kruskal–Wallis chi-squared = 160.35, d.f. = 33, $p < 2.2 \times 10^{-16}$). Wolves from Pleistocene Belgium (mean = 263 mm), and Neolithic (mean = 245 mm) and modern (mean = 239 mm) France are in the same cranium size range, with a visible size reduction through time (figure 3), although no significant differences were found among these three groups (electronic supplementary material, table S6). With the exception of one individual from Eliseevichi (256 mm), ‘protodogs’ have shorter crania (mean = 229 mm) than broadly contemporaneous Pleistocene wolves, yet the differences are not significant (electronic supplementary material, table S6). The Mesolithic dog from Portugal (Muge) has a shorter cranium than all the wolves, while Mesolithic dogs from Siberia (Zhokhov) are within the lower range of the ‘protodogs’ and modern wolves. The Pleistocene ‘protodogs’ from Belgium (Goyet) and France (La Baume Traucade) are within the lower cranium size range of modern wolves from France. Neolithic dogs from western Europe have shorter skulls than Mesolithic dogs from across Eurasia and are significantly shorter than dingoes but not village dogs. Chalain dogs have a similar size range to terrier dogs, but their cranium is not as reduced as those of toy dogs. Because of the extreme skull size reduction in toy dogs, and the relatively recent emergence of this phenotype, we excluded this group from the following analyses of relative ECV across modern and ancient canids.

5.2. ECV variation in modern and ancient dogs and wolves

ECV variation differs greatly across modern and ancient wolves, dingoes and dogs (figure 4; Kruskal–Wallis chi-squared = 137.56, d.f. = 14, $p < 2.2 \times 10^{-16}$). In this distribution, all dogs (dingoes, village dogs, dog breeds and Late Neolithic dogs) have significantly smaller (32%) ECV than all wolves (Pleistocene, Neolithic and modern; electronic supplementary material, table S7), which remains true when also considering only modern dogs (including dingoes) and wolves. The ECV of wolves across Pleistocene (mean = 153.6 mm^3), Late Neolithic (mean = 140.45 mm^3) and modern (mean = 133.71 mm^3) periods ranges between 111 mm^3 and 172 mm^3, with a visible reduction over time. ECV values from Late Neolithic wolves (Chalain) are not significantly different from those of modern wolves (electronic supplementary material, table S7) and are in the range of Pleistocene ‘protodogs’ from Belgium (Goyet) and France (La Baume Traucade).

ECV varies greatly among the different dog lineages (i.e. dingoes, and village and breed dogs) (figure 4) though we only found a significant difference between the largest ECV of working dogs (mean = 111.17 mm^3) and the smallest ECV of toy dogs (mean = 60.14 mm^3) (electronic supplementary material, table S5). Dingoes (mean = 92.47 mm^3) display significantly larger ECV than village dogs (mean = 79.94 mm^3) but are within the ECV range of dog breeds, between the largest working dog (138 mm^3) and the smallest toy dog (47.6 mm^3). In this wide distribution, the Late Neolithic dogs of Chalain fall between village dogs and toy dogs, at the lowest end of the terrier range with a 46% ECV reduction compared to modern and Neolithic wolves. Seven of the eight Chalain dogs have an ECV similar to modern medium spitz, cocker spaniel, pug and collie, and one has the same ECV as toy dogs like chihuahua and Pekingese breeds (electronic supplementary material, figure S1).

5.3. rECV variation in modern and ancient dogs and wolves

TL explains approximately 64% of the ECV variation ($R^2 = 0.636$, F-statistic = 213.7, d.f. = 121, $p < 2.2 \times 10^{-16}$), while the foramen magnum breadth (FMb) explains approximately 52% ($R^2 = 0.518$, F-statistic = 75.08, d.f. = 68, $p < 0.0001$). The variation of rECV across modern wolves and dogs (figure 5A) shows that wolves have significantly greater rECV than dogs (electronic supplementary material, table S8). The Goyet ‘protodog’ also displays greater rECV than the Pleistocene and Postglacial (Trou des Nutons and Trou Balleux), Late Neolithic and modern wolves of similar cranium length (figure 5B). On the other hand, La Baume Traucade Pleistocene ‘protodog’ shows rECV values comparable to those of modern French wolves.

To compare the rECV across ancient and modern dogs and wolves, we excluded toy dogs as well as pugs and French bulldogs as these very small and extremely brachycephalic dogs are clear outliers. We found no significant rECV differences across dingoes, village dogs and the functional groups of dog breeds (electronic supplementary material, table S8). Nevertheless, working dogs show, on average, higher rECV than other functional groups (figure 5A). The rECV values of dingoes are similar to those of mesocephalic breeds of dogs of the same skull size but larger than those of village dogs of the same skull size (figure 5A, B, C). Finally, the Neolithic Chalain dogs show smaller rECV than dingoes and mesocephalic dogs to a lesser extent but similar rECV values to village dogs (figure 5A, B, C).

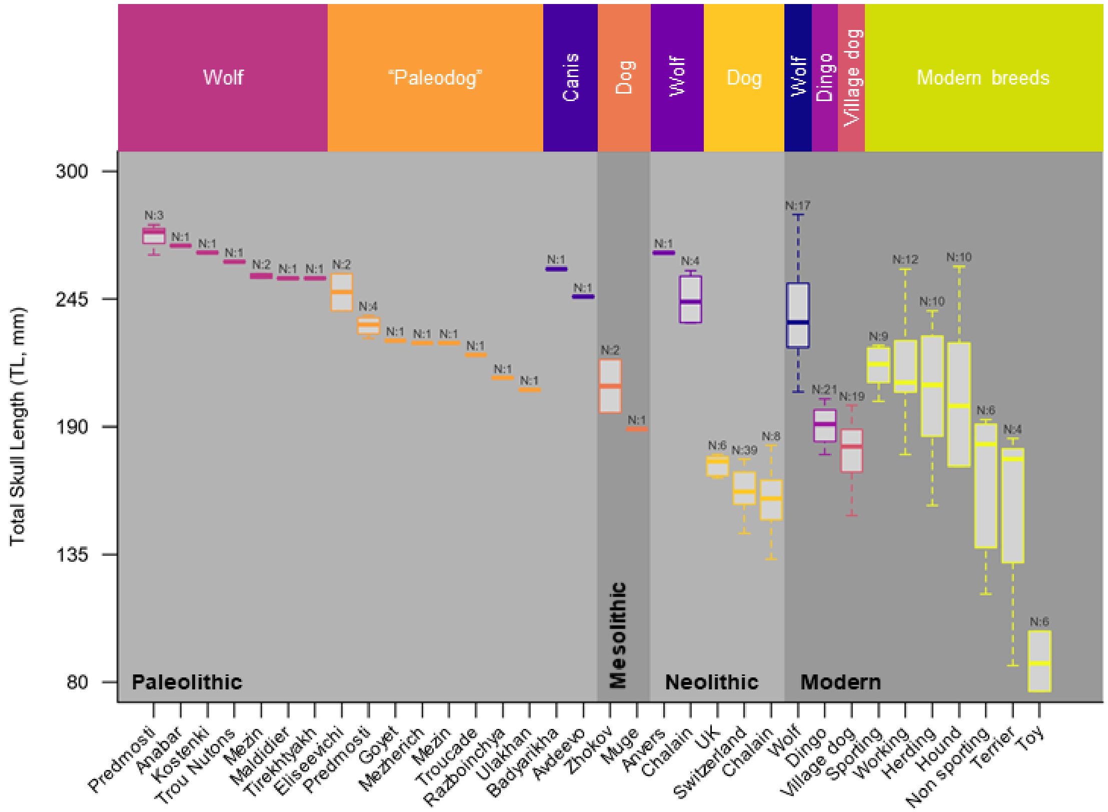

Figure 3. Boxplot of TL variation in wolves and dogs across Pleistocene, Mesolithic, Neolithic and modern periods. For each group and period, the TL values are displayed in a descending order. TL values include data from this study and from the literature (see electronic supplementary material, table S4). Palaeolithic '*Canis*' from Badyarikha and Avdeevo are specimens without identification as wolf or 'protodog'. Dog breeds are grouped according to their AKC classification, which reflects their traditional function.

5.4. Neurocranial anatomy in ancient and modern dogs and wolves

We compared neurocranial variation across ancient and modern wolves and dogs, using a scatterplot of their ECV against their cephalic index (CI) values (figure 6), excluding toy dogs, pugs and the French bulldog. In this dataset, the CI showed no significant relationship with endocranial volume (F-statistic = 0.515, d.f. = 114, $p = 0.474$). The scatterplot shows that Pleistocene wolves from Les Nutons and the protodogs from Goyet and La Baume Traucade cluster with modern and Neolithic wolves. Dingoes, village dogs and the Chalain dogs cluster together, with the Chalain dogs showing greater similarity to village dogs and some mesocephalic herding breeds (e.g. rough collie and Australian shepherd dog) than to dingoes.

6. Discussion

Advances in endocast imaging (e.g. [34]) have enabled us to accurately estimate brain size in 22 archaeological and palaeontological canid specimens. Through this, we could track how brain size changed during different phases of the evolutionary history of dogs. We found that so-called 'protodogs' from the Pleniglacial period in Belgium (Goyet) and the Late Glacial period in France (Baume Traucade) show no brain size reduction and possess a neurocranial anatomy most similar to Pleistocene, Neolithic and modern wolves. This would strongly support their identification as wolves, following previous studies which proposed that western European Pleniglacial dogs are part of an ecophenotypic diversity of Pleistocene wolves that is now extinct [47,48], although this interpretation depends on the comparative framework and methods used (see [49,50]). Yet, we found that the Goyet 'protodog' shows a larger relative brain volume than Pleistocene, Neolithic and modern wolves of comparable skull size, suggesting that, if we accept that this specimen was indeed a 'protodog', brain size increases, rather than decreases, might have occurred during the intensification of human and

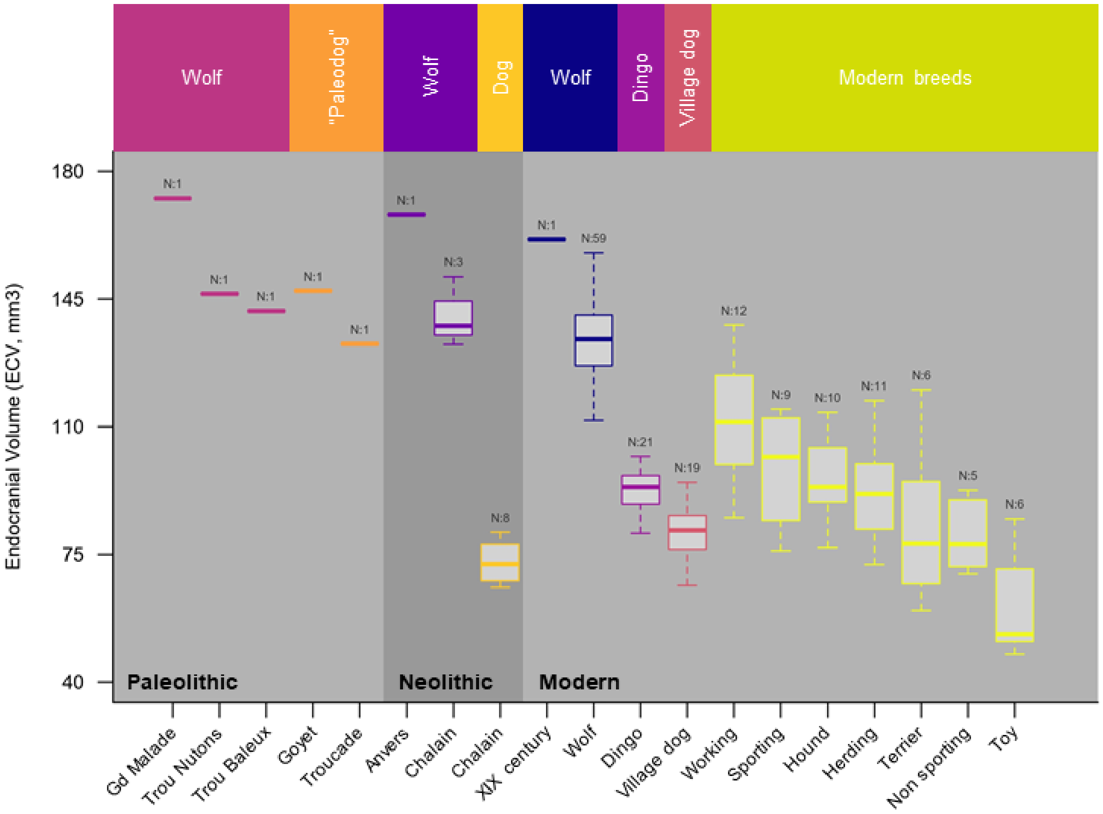

Figure 4. Boxplot of ECV variation across ancient (Palaeolithic and Neolithic) and modern wolves, dingoes, and dogs (village dogs and modern breeds). Dog breeds are grouped according to the AKC classification, which reflects their traditional function.

wolf interactions at the beginning of the domestication process. This is supported by recent neuroanatomic analysis of grey foxes of the fox-farm experiment [51], which showed that the ones selected for tameness displayed a greater amount of grey matter in the frontal cortex [52]. Pleiotropic consequences of behavioural selection may have also contributed to this brain size increase in 'protodogs'. The first would be the cognitive challenges of the new human environment [53] and the behavioural flexibility required to fit into the human social environment [54], as evidenced for small mammals adapting to urbanization [55]. The second could have been the greater access to food resources, as evidenced in captive Mexican wolves, which display greater brain volume than their free-ranging counterparts [56]. Indirect behavioural selection, new allospecific interactions, new cognitive socio-environmental challenges or greater access to energy resources could all have led to an increase in brain volume in 'protodogs'; however, this remains to be explored.

Our study recapitulates the brain size reduction previously identified between modern wolves and dogs [8,9], with a threefold reduction in endocranial volume between the smallest- and the largest-brained breed of dogs. Despite this reduction, we found that working dogs show greater ECV than dingoes, village dogs and dog breeds, even when accounting for body size, suggesting that working dogs have larger brains than other functional groups. This trend differs from a recent study which reported working dogs as having the smallest rECV of all dogs [8]. These discrepancies may reflect the increased number of large dogs in the working group in our study and a different statistical approach to compute the relative ECV. Nonetheless, our results tend to be in agreement with evidence that greater brain volume predicts cognitive performance and self-control [57] and underlies the greater trainability observed in working dogs [58,59]. However, the AKC's working dog functional categorization covers a wide range of jobs, which may result in differences of behaviour and cognitive performance being overlooked [60].

We observed major body size reduction between the Mesolithic and the Neolithic dogs (figure 3), with Chalain dogs exhibiting a mesocephalic cranial morphology typical of free-ranging village dogs and a skull size close to Terrier dogs like medium-sized German spitz, resembling other Neolithic dogs found in the UK and Switzerland (figure 3). This is concordant with the occurrence of a relatively homogeneous morphotype of small dogs in the Middle and Late Neolithic of western Europe [61–63]. Along with this drastic body size reduction, we found that the brain size reduction in dogs compared

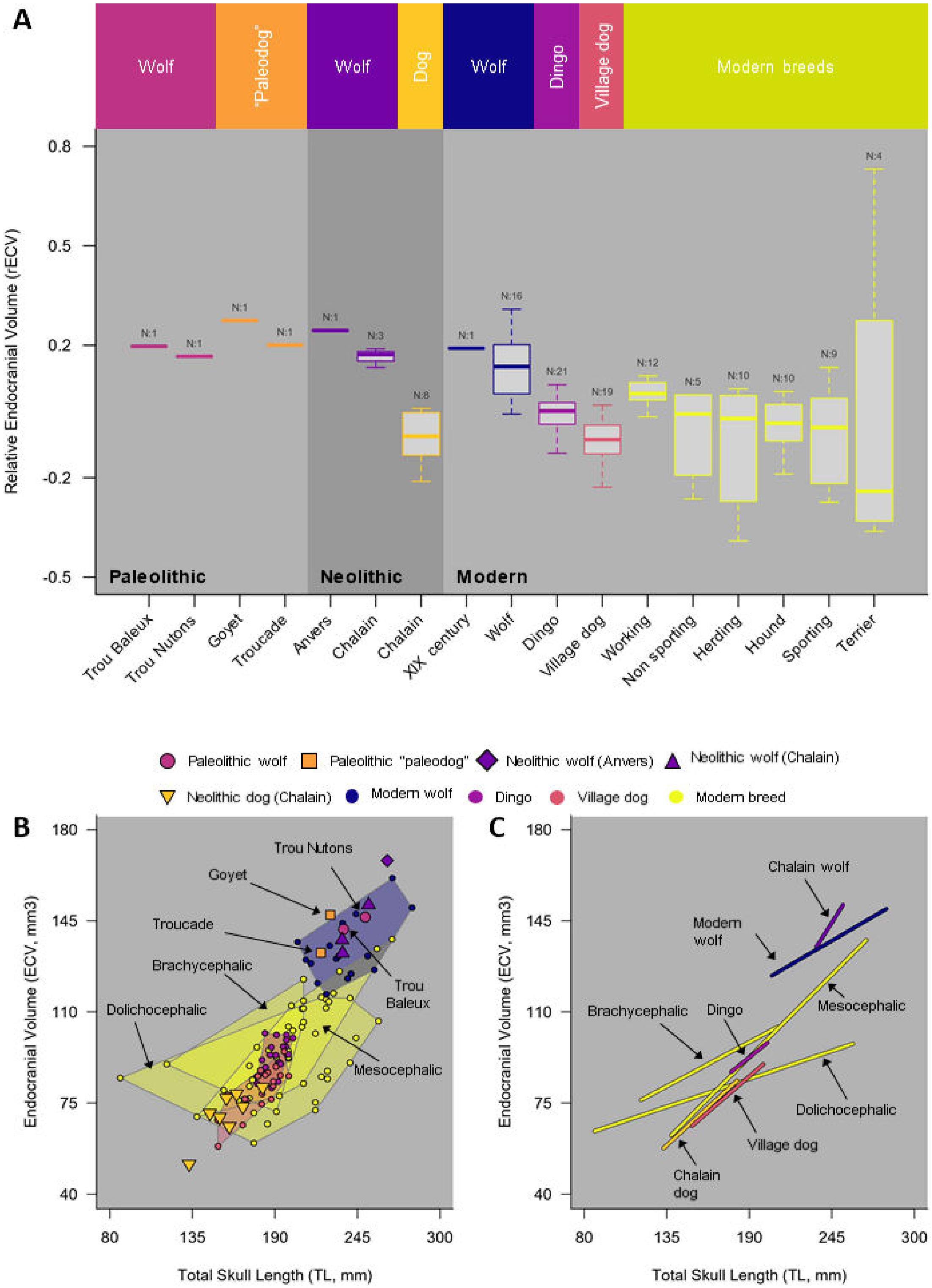

Figure 5. Variation in rECV (residuals from the regression of ECV on cranium length) across ancient (Palaeolithic and Neolithic) and modern wolves and dogs. (A) Boxplot of rECV values with modern dog breeds grouped by AKC functional categories. (B) Scatterplot of ECV against cranium length (TL). (C) Same scatterplot with only the slopes of the linear regression performed on groups with more than two specimens.

with wolves was already established by the Late Neolithic 5000–4500 BP. In fact, this difference was larger than that observed between modern wolves and dogs, with Chalain dogs displaying a 46% smaller brain size than Neolithic wolves, comparable to small terrier and toy breeds such as the pug, chihuahua and Pekingese. These results suggest that selection for small dogs may have begun in Europe during the Neolithic period, and possibly before the emergence of giant flock-guardian dogs,

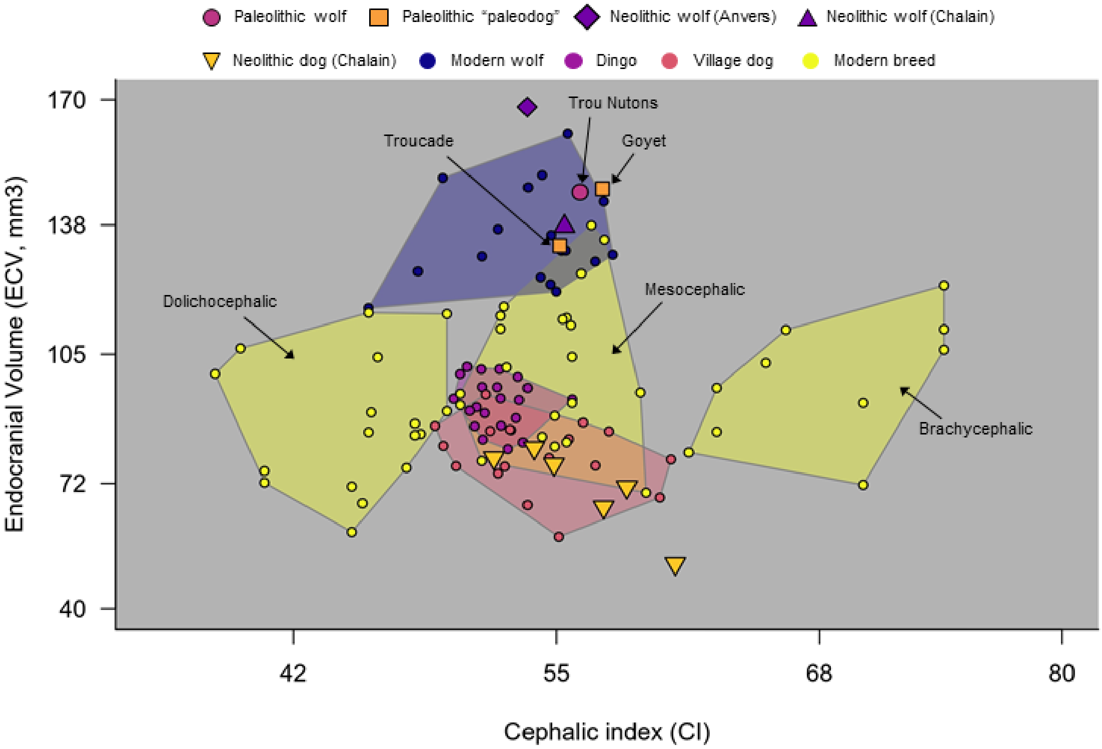

Figure 6. Neurocranial variation in modern and ancient wolves and dogs (excluding toy dogs such as pugs and French bulldogs). Scatterplot of the endocranial volume (ECV in mm^3) against the CI.

which are often regarded as the first morphotype to appear independently in different regions of the world [35]. To further document the timing and the cultural contexts of these changes, more Mesolithic and Neolithic dogs across Europe need to be examined.

This drastic brain size reduction in these small Late Neolithic dogs also suggests accompanying behavioural changes. Indeed, recent studies have shown that small dogs tend to be more fearful, aggressive towards strangers, prone to barking [46,59,64,65] and less trainable [33,66]. The latest neuroanatomical studies explain these behavioural differences by the reorganisation of the brain tissues induced by the change in brain size [19,29]. Brain size decrease is linked to the reduction of the cortical brain, along with an increase in subcortical tissues. This brain tissue reorganization induced by size reduction means less cognitive abilities and more anxiety-driven behaviours. This suggests that the small-brained Neolithic dogs of Chalain were likely more fearful, anxious, prone to barking and not very trainable, raising questions about their role in this Late Neolithic farming socio-ecosystem.

Zooarchaeologists have already proposed that Middle and Late Neolithic dogs in this region served polyvalent purposes, including symbolic and ornamental roles with no clear economic or utilitarian role [37]. Their use in ritual feasting has also been suggested for Neolithic contexts in Italy [67]. Given the strong neurocranial similarity between the Chalain dogs and present-day pariah-type village dogs, the latter may provide an analogy for their purpose, while their small brain size provides insight into their temperament. The dogs of Chalain were likely part of the Neolithic settlement socio-ecosystem, like village dogs, scavenging food refuse and potentially used as a convenient source of meat, like in many parts of the world today, such as eastern and southeastern Asia (e.g. [68–70]). The dog bones from Chalain were found disconnected and among the other faunal remains consumed by the village settlers [32], which would support this interpretation. We also speculate that these small Neolithic village dogs could have served the purpose of alerting for any unexpected changes in the settlement surroundings, given their inferred anxious temperament and higher reactivity to novelty. Like modern village dogs, their poor diet and harsh living conditions may have also imposed metabolic constraints on their growth [71,72], contributing further to their small brain size. One might then ask whether this highly anxious and reactive temperament could have been one of the main targets of dog selection during the Neolithic.

Finally, we found that dingoes display an endocranial volume that is intermediate between the largest- and smallest-brained dogs but greater than village dogs of the same skull size. Despite reverse trends documented in feral mink populations [73], these results suggest the absence of reversibility of brain size reduction by domestication through feralization [74,75]. Yet, this increase relative to village dogs is consistent with previous large-scale studies comparing the relative brain size of dingoes with dogs and other wild canids, suggesting that brain size increases in dingoes could be linked to their evolution as apex predators in the Australian environment [76]. Reduced metabolic constraints of placental predators in an environment of marsupial mammals, along with the behavioural flexibility required by the cognitive challenges of the Australian environment, could have been strong evolutionary constraints as well [7], supporting recent claims that dingoes are on a distinct evolutionary trajectory when compared with other dogs [77].

7. Conclusion

Our results provide new evidence for changes in brain size during the evolutionary history of dogs. We found no evidence of brain size reduction in 'protodogs' of the Upper Pleistocene. Instead, we raise the possibility that the intensification in humans and canids interaction may have led to a slight increase in brain size, reflecting the adaptation to the cognitive challenges of living in proximity to humans, or easier access to food resources. This study found, however, a dramatic 46% brain size reduction by 5000–4500 yr BP in Late Neolithic dogs compared with contemporaneous wolves, with brain volume close to that of recent Toy breeds, providing potential evidence for very early behavioural selection. Relying on the latest understanding in the link between neuroanatomy and dogs' temperament, this drastic brain size reduction in the Neolithic provides important clues for their potential use for alerting the settlement against threats, among other functions such as scavenging, a convenient source of meat or hunting. Both interpretations require further testing with more samples of Palaeolithic, Mesolithic and Neolithic wolves and dogs from Europe. Furthermore, endocranial volume is only a proxy for brain anatomy that does not account for changes in brain proportions or more localized changes driven by natural and artificial selection for behavioural specialization to specific anthropogenic environments [78]. Addressing this hypothesis, however, will require future studies to explore more aspects of complex anatomical features of the endocast and its integration with the skull [79], using the latest developments in the quantitative methods for anatomy [80]. Such an approach will allow the exploration and disentanglement of smaller scale anatomical changes associated with behavioural changes during different stages of dog domestication, including the initial transition from wild to domestic and later adaptation to the multitude of anthropogenic environments to which dogs have been exposed over their long co-evolution with people.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data, script and metadata supporting this article are available in the Data. InDoRES Repository [81]. Supplementary material is available online [82].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. T.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, validation, visualization, writing—original draft, writing—review and editing; L.-M.H.: formal analysis, investigation; A.V.: investigation, methodology, software, visualization, writing—review and editing; M.M.: resources, writing—review and editing; C.B.: resources, writing—review and editing; R.-M.A.: resources, writing—review and editing; P.P.: resources, writing—review and editing; M.G.: resources, writing—review and editing; E.C.: resources, writing—review and editing; F.E.: resources, software, writing—review and editing; K.C.: data curation, resources, writing—review and editing; L.Z.G.: resources, writing—review and editing; E.K.: resources, writing—review and editing; N.K.: resources, writing—review and editing; T.C.: resources; J.J.: resources; S.L.: resources; C.G.: project administration, resources, writing—review and editing; M.F.: resources; C.D.: resources; A.H.: resources, writing—review and editing; L.K.: funding acquisition, resources, writing—review and editing; T.J.P.: resources; L.S.: resources, visualization, writing—review and editing; L.F.: writing—review and editing; J.M.-M.: resources, writing—review and editing; S.L.: writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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