Received: 29 November 2020 | Revised: 23 February 2021 | Accepted: 24 February 2021

DOI: 10.1002/ar.24624

The Anatomical Record
Advances in Integrative Anatomy and Evolutionary Biology

WILEY

COMMENTARY

Morphology-based diagnostics of "protodogs." A commentary to Galeta et al., 2021, *Anatomical Record*, 304, 42–62, doi: 10.1002/ar.24500

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Abstract

In a recent article in this journal, Galeta et al., (2020) discussed eight Pleistocene "protodogs" and seven Pleistocene wolves. Those "protodogs" had been diagnosed in earlier publications, based on skull morphology. We re-examined the Galeta et al. paper to offer comments on their observed outcomes, and the conclusion of presumed domestication. Of seven metrics that the authors used, five differed statistically between their two groups. However, from more elaborate studies, some of those same metrics had been rejected previously as not valid species-distinguishing traits. In this respect, we do accept cranium size and wider palate as species-distinguishing metrics. The physical size of their specimens was much larger than other archaeological specimens that have been accepted as dogs. Additionally, their sample size was small, compared to the number of available specimens, as shown from previous publications by the same group. Thus, we considered statistical differences that were found between groups in their study, and assessed whether the outcomes could have resulted from natural morphological variation. We examined a group of 73 dire wolves ((Aenocyon [Canis] dirus; Perri et al., 2021), using the same methods as used by Galeta et al., (2020). We could segregate two distinct morphological groups in our study, one having outcomes that were identical to the "protodogs" in Galeta et al. (2020). For the specimens of extinct dire wolves to segregate in the same way as the subjects from Galeta et al. indicates that natural variation probably was the driver of their observed outcomes, domestication being an unlikely assumption.

KEYWORDS

cranium, dog, domestication, morphology, pleistocene

1 | INTRODUCTION

In a recent Anatomical Record article "Morphological evidence for early dog domestication in the European Pleistocene: New evidence from a randomization approach to group differences" by Galeta, Láznicˇková-Galetová, Sablin, and Germonpré (2021), the authors report on eight "protodogs" and seven Pleistocene wolves from previous publications (Germonpré et al., 2009, 2017; Germonpré, Laznickova-Galetova, & Sablin, 2012; Sablin & Khlopachev, 2002). They applied complicated statistics and the data were analyzed—after size-adjustment and log transformation—using cluster analysis that was followed by linear discriminant analysis. Their results, they claim, add new evidence to show that these two groups differ significantly and conclude that "protodogs" show (among other metric differences) shorter crania and wider snouts, which would be typical for domestication.

Morphometry often has been used to distinguish the earliest dogs in the archaeological record (Ameen et al., 2017; Janssens et al., 2016, 2019, 2019a; Napierala & Uerpmann, 2012; Pitulko & Kasparov, 2017; Sablin & Khlopachev, 2002; Studer, 1901; Wolfgram, 1894). Several differences between dogs and wolves have been suggested as species-diagnostic, many of these now have been rejected for that purpose (for an overview, see Janssens, Perri, et al., 2019). Diagnosing the earliest archaeological dogs is mainly based on size reduction (Aaris-Sorensen, 1977; Benecke, 1987, 1994; Dimitrijević & Vuković, 2012; Hemmer, 1990; Morey, 1992, 1994, 2010; Rütimeyer, 1861; Studer, 1901; Wolfgram, 1894), which is isometrically related to cranium length (Losey, McLachlin, Nomokonova, Latham, & Harrington, 2017; Tchernov & Horwitz, 1991; Wayne, 1986). Other acceptable discerning metrics are: wider snout ratio, higher skull ratio, shorter carnassials, larger orbital angle, smaller brain index and inner ear differences; but also archaeological context and genetics are important factors (Bergstrom, Frantz, Schmidt, Ersmark, et al., 2020; Janssens et al., 2016; Janssens, Perri, et al., 2019; Janssens, Gunz, et al., 2019; Larson et al., 2012; Pitulko and Kasparov, 2018; Thalmann et al., 2013; Zeder, 2012). About 20 Pleistocene specimens are generally accepted as the earliest archaeological dogs which are considerably smaller than contemporary wolves (about 1/3).The oldest finds up to now, are 14.5 kya old (Perri et al., 2021; Table 1 and references therein).

Since 2009 much older specimens (up to 34 kya) were suggested to be insipient or "protodogs" (Germonpré et al., 2009, 2012, 2017; Table 2). Assigning these as wolf specimens that underwent anthropogenic morphological change, was mainly based on shorter cranium, shorter snout, shorter mandible metrics and wider snout. Also change in diet (isotopes) and dental wear was reported to be different (Bocherens et al., 2014; Prassack, Dubois, Laznickova-Galetova, Germonpré, & Ungar, 2020).

"Protodogs" as a signal of earlier domestication, have been contested by many, mainly based on lack of genetical closeness to dogs (Thalmann et al., 2013), lack of important size reduction, doubts about real differences in diet and dental wear, doubts about the validity of discerning metrics and on methodology (Ameen et al., 2017; Boudadi-Maligne & Escarguel, 2014; Crockford & Kuzmin, 2012; Drake, Coquerelle, & Colombeau, 2015; Janssens, Boudadi-Maligne, Mech, & Lawler, 2021; Janssens, Perri, et al., 2019; Jung & Pörtl, 2018; Ledoux & Boudadi-Maligne, 2015; Mech & Boitani, 2003; Morey, 2010; Morey & Jeger, 2015; Napierala & Uerpmann, 2012; Perri, 2016; Pitulko & Kasparov, 2017; Wilczynski, Goslar, Wojtal, et al., 2020).

In this study, we also question whether the morphological variation between the two groups depicted by Galeta et al. (2021) is related to domestication process. Next, we question the value of the metrics used in Galeta et al. (2021) find evidence for early signs of domestication. Last, we focus on the small group size examined, already reported as problematic, by the authors themselves.

To investigate the first question, we examined a group of dire wolves (*Canis dirus*; Perri, Mitchell, Mouton, et al., 2021) with the same metrics and statistical methods as in Galeta et al. (2021). We postulate that if we can show identical separation of two subgroups, this subdivision might equally be the result of natural variation, and not necessarily related to an ellry signature of domestication. Our main aim is to increase awareness of the fact that interpretation of morphological variation in small samples should be done with great care and an open mind for alternative explanations.

2 | MATERIALS AND METHODS

We evaluated the same seven metrics that were used by Galeta et al. (2021). Our study group was a set of 73 dire wolves from O'Keefe et al., (2014). The specimens are from the Hancock Collection at Page Museum, La Brea Tarpits, Los Angeles CA (pits 91, 13, 61/67), and from the University of California Museum of Paleontology, Berkeley CA (pit 3874). The time period covered by the specimens ranged 28–13 kya. The measurements were taken from digitalized photographs (TPSdig).

The metrics that were examined included (vdd, von den Driesch, 1976): (1) Total cranium length TL, from landmark 1–4 (vdd 1); (2) Viscerocranium (snout) length VL, from landmark 1–2 (vdd 8); (3) Alveolar length AL of the tooth row P1–M2, landmark 13–16 (vdd 15); (4) P4 mesio-distal diameter, from landmark 14–15 (vdd 18);

TABLE 1 Earliest Late-Pleistocene and transitional period to early Holocene small stature dogs

Specimens	Chronocultural context	Direct dating on dog remains	Indirect datings	mtDNA clade	Country	MNI	References
Erralla	Lower/Upper Magdalenian		12,310 ± 190/16,270 ± 240		Spain	1	Altuna, Baldeon, & Mariezkurrena, 1984; Vigne, 2005
Montespan	Middle Magdalenian		*ca 13,500/15,500*[a]		France	1	Pionnier-Capitan et al., 2011
Le Morin	Upper Magdalenian	OxA-23,627:12,540 ± 55 OxA-23,628:12,450 ± 55			France	1	Boudadi-Maligne, Mallye, Langlais, & Barshay-Szmidt, 2012
Bonn-Oberkassel	Upper Magdalenian	KIA-41161:12,110 ± 45; KIA-41162:12,210 ± 60; KIA-41163:11,620 ± 60; OxA-4793:12,270 ± 100		C	Germany	2	Street, 2002; Janssens et al., 2018
Kesslerloch	Upper Magdalenian	KIA-33350:12,225 ± 45		C	Switzerland	1	Napierala and Uerpmann, 2010
Grotta Paglicci	Epigravettian	OxA-26,316:12,175 ± 55	?		Italy	1	Boschin et al., 2020
Grotta Romanelli	Final Epigravettian		8048 ± 75/11,858 ± 85	C	Italy	1	Boschin et al., 2020; Calcagnile et al., 2019
Le Closeau	Azilian		12,050 ± 100/12,480 ± 70		France	1	Pionnier-Capitan et al., 2011
Troubat	Azilian	OxA-36,550:10,600 ± 45			France	2	Boudadi-Maligne et al., 2020
Palegawra	Zarzian		*ca 12000*[a]		Iraq	1	Turnbull & Reed, 1974
Pont d'Ambon	Laborian	GifA 99,102:10730 ± 100 Beta 411,309:10,130 ± 40		C	France	2	Célérier, Tisnerat, & Valladas, 1999; Pionnier-Capitan et al., 2011; Boudadi-Maligne, Bonnet-Jaquement, Langlais, Ferrie, & Mallye, 2018
Saint-Thibaud-de-Couz	Laborian	Ly23/OxA-4405:10,050 ± 100			France	1	Chaix, 2000
Kartstein	Ahrensburgian		9995 ± 65/10,220 ± 75	C	Germany	1	Baales, 1992; Charles, 1993
Bedburg	Early Mesolithic		9,600 ± 100/9,780 ± 100		Germany	1	Street, et al., 2015
Senckenberg-Moor	Mesolithic		*ca 10000*[a]		Germany	1	Mertens, 1936; Degerbøl, 1961
Ain Mallaha	Natufian		10,530 ± 100/10,540 ± 90		Israel	2	Tchernov & Valla, 1997; Grosman, 2013
Hayonim Terrace	Natufian		9,640 ± 100/11,790 ± 120		Israel	2	Tchernov & Valla, 1997; Grosman, 2013

(Continues)

TABLE 1 (Continued)

Specimens	Chronocultural context	Direct dating on dog remains	Indirect datings	mtDNA clade	Country	MNI	References
Shillourokambos	Neolithic (Middle PPNB)		9,432 ± 49/9,525 ± 49		Cyprus	1	Vigne, et al., 2011
Shubayqa 6	Neolithic (PPNA)		9,440 ± 50/10,072 ± 43		Jordan	?	Yeomans et al., 2019
Tell Mureybet	Late Natufian (Khiamian)		9,945 ± 50/9,905 ± 60		Syria	1	Helmer, 1991; Gourichon and Helmer, 2008; Ibáñez, 2009; Grosman, 2013
Uncertain dog remains							
Monruz	Upper Magdalenian		12,800 ± 85/13,330 ± 110		Switzerland	3?	Brochier & Moulin, 2010; Müller & Leesch, 2013
Hauterive	Upper Magdalenian		12,510 ± 130/13,050 ± 155		Switzerland	1	Morel & Müller, 1997; Brochier & Moulin, 2010

[a] *italics* = indirect dating on site, but not on level in which dog remains were found.

(5) Greatest braincase width GWBRC, from landmark 21 to midline (vdd 29), and duplicated; (6) Greatest palatal width GWPAL, from landmark 15 to midline (vdd 34), and duplicated; (7) Smallest snout width MWPAL, from landmark 13 to midline (vdd 35), and duplicated.

Smallest snout width, as measured with the landmark method, differs minimally from the vdd 35 metric. The other six metrics, based on landmarks, are congruent with vdd metrics as in Galeta et al. (2021).

In our first step of statistical analyses, a hierarchical clustering was performed on the size-corrected log-transformed Euclidian distances. More specifically, a Ward's hierarchical agglomerative clustering method is used in Galeta et al. (2021) (Murtagh & Legendre, 2014) was applied. In this way, dissimilarities in shape between the craniums were contrasted such that craniums of different shape end up in separate clusters or groups. The size correction was performed using the residuals from a standard major axis analysis, with trait size as dependent variable and centroid size of the cranium as explanatory variable, both being log-transformed (see Galeta et al. [2020] for an identical approach). Next, the significance of shape difference was tested using an MANOVA test, and a linear discriminant analysis (DA) was performed to evaluate the number of crania, assigned to the correct hierarchical cluster, using a cross validation approach. Finally, the differences in trait values were tested, using an ANOVA test (*F*-test) and calculated as effect sizes, based on the standardized means and standard deviations. Effect sizes were expressed as Cohen's *D*. To ease the interpretation of these effect sizes, they are often defined as being small when *D* is smaller than 0.2, medium or intermediate when values of *D* are around 0.5 and large for values of *D* above 0.8.

3 | RESULTS

The hierarchical clustering in dire wolves (Figure 1), reveals a separation in two subgroups (indicated by red rectangles, Figure 1). Morphological shape was significantly different between the two groups (MANOVA; Figure 1, $F_{7,65} = 17.9$, $p < .0001$). The linear discriminant function (based on DA), assigned 90% of the craniums to the correct group, thus scores show only little overlap (Figure 2), indicating good group separation.

A significant difference between the two groups was found for five metrics:

1. Total cranium length (TL) (vdd 1);
2. P4 mesio-distal diameter;
3. Greatest width of the brain case (GWBRC) (vdd 29);
4. Greatest palatal width (GWPAL) (vdd 34);
5. Minimal width of the palate/snout (MWPAL) (vdd 35).

TABLE 2 Pleistocene canids used in studies on "protodogs"

A. Pleistocene wolves (or defined unknown)			
Germonpré et al., 2009	**Germonpré et al., 2012**	**Germonpré et al., 2017**	**Galeta et al., 2020**
	Kostenki 17 36233	Kostenki 17 36233	Kostenki 17 36233
		/	/
		/	/
		/	/
	Predmosti 1924	Predmosti nr=?	Predmosti nr=?
	Predmosti 1	/	/
Trou des Nutons 2559	Trou des nutons 2559	Trou des nutons 2559	Trou des nutons 2559
Mezin 5469	Mezin 5469	Mezin 5469	Mezin 5469
Mezin 5488	Mezin 5488	Mezin 5488	Mezin 5488
		Anabar	Anabar
Trou Bailleux	/	/	/
Trou de la Naulette[a]	/	/	/
Grand Malades[a]	/	/	/
Yukatia 29699?	Yukatia 29699	/	/
		Tirehtyakh	/
		Razboinychia	/
		Maldidier	Maldidier
Plesitocene canids defined as unknown			
	Predmosti 1062	Badyarikha	
	Predmosti 1061		
Avdeevo 911	Avdeevo 911		
B. "Protodogs"			
Germonpré et al., 2009	**Germonpré et al., 2012**	**Germonpré et al., 2017**	**Galeta et al., 2020**
Goyet	Goyet	Goyet	Goyet
	Predmosti 1060	Predmosti 1060	Predmosti 1060
	Predmosti 1069	Predmosti 1069	Predmosti 1069
	Predmosti-	Predmosti-	Predmosti-
Elliseevichi 447	Elliseevichi 447	Elliseevichi 447	Eliseevichi 447
Elliseevichi 23781	Elliseevichi 23781	Elliseevichi 23781	Elliseevichi 23781
Mezin 5490	Mezin 5490	Mezin 5490	Mezin 5490
Mezerichi 4493	Mezerichi 4493	Mezerichi 4493	Mezerichi 4493
		Ulakhan Sular	/

Note: "/" specimens from former studies not used in more recent studies by same authors.

[a] Mousterian layers relater to Neanderthal finds.

Effect sides (Cohen's *D*) were medium-to-very large for these significant effects. The crania in dire wolf group 2 can be characterized as having: shorter, wider cranium and wider palate (Table 1). The morphological differences between "protodogs" and Pleistocene wolves in Galeta et al. (2021) were greater for TL, VL, and AL compared to the differences in dire wolves. For the GWBRC, GWPAL and MWPAL, differences were comparable, or greater, in dire wolves, compared to Galeta et al. (2021).

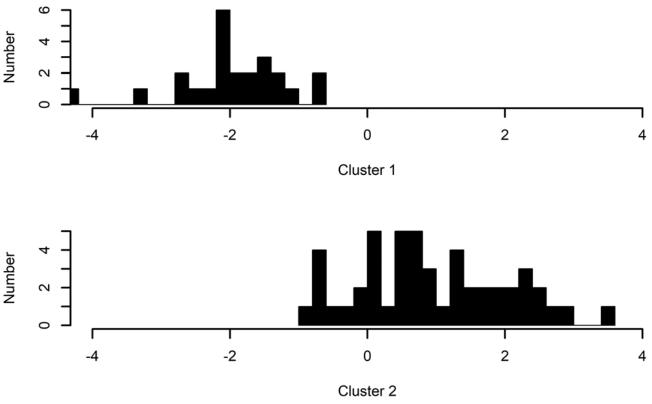

FIGURE 1 Cluster analysis dendrogram based on log-transformed size corrected distance measures. Two clusters are highlighted by the two rectangles. Morphological differences between both clusters were highly significant (MANOVA: $F_{7,65} = 17.9$, $p < .0001$)

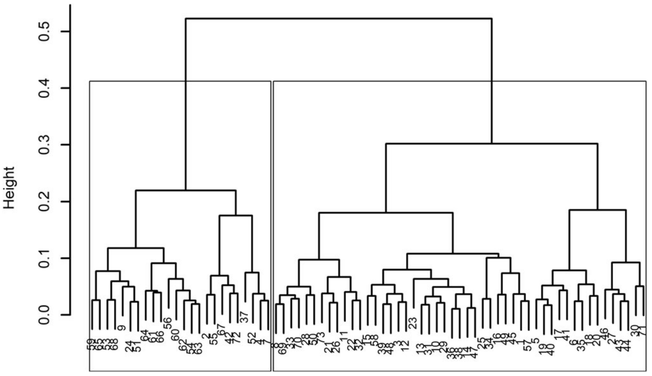

FIGURE 2 Histograms of scores of the linear discriminant function from the discriminant analysis separating the two clusters from the cluster analysis. Out of the 24 wolves in cluster 1, 22 (92%) were assigned correctly using cross validation. Out of the 49 wolves in cluster 2, 44 (90%) were assigned correctly using cross validation. Thus, in total 90% (66 out of 73) of the skulls were assigned to the correct cluster on the basis of the linear discriminant analysis

4 | DISCUSSION

The primary topics to discuss are: (a) is the variation between the two groups related to domestication; (b) what is the value of the metrics used to test for domestication; and (c) problems with small group size.

5 | MORPHOLOGICAL VARIATION BETWEEN THE TWO GROUPS

The most important conclusion of our analysis is that dire wolves could be segregated into two groups, one with a "typical domestication signature." The primary reason that we chose a dire wolf comparison was an available database with all of the metrics that were used by Galeta et al. (2021). Additionally, dire wolves are highly similar to Pleistocene wolves in physiognomy and morphology (Perri, Mitchell, et al., 2021), and their dating in this studied group is Upper Pleistocene.

Since dire wolves were never domesticated, the implication is that group segregation is likely reflecting normal population variation, which should also be considered in the context of any biometric study. As thus, the documented morphological variation in Pleistocene large canids could also reflect natural variation in the absence of any domestication event. The word "protodogs" should thus be used with great caution and perhaps be rephrased as "Pleistocene large canids with dog-like skull features."

Galeta et al. (2021) added modern specimens in the study and show that also modern wolves and dogs can be separated statistically by using their method. These modern samples enlarge examined groups but add no fundamental information on whether or not the two Pleistocene small groups really differ due to natural selection caused by domestication. We are not convinced of the benefit, nor correctness, of adding recent specimens in the analyses, as wolves evolved morphologically since the Pleistocene, they are smaller (Kurtén, 1965), and have more gracile crania (Janssens, Perri, et al., 2019). In addition, with so few ancient large canids being measured, a discriminant analysis tends to overfit when comparing several groups.

6 | VALIDITY OF THE METRICS USED TO TEST FOR DOMESTICATION

Of the seven parameters used by Galeta et al. (2021) five differ between groups: cranial length; viscero-cranial length; maxillary tooth row length; braincase width and minimal palate width.

6.1 | Cranium length (TL)

Cranium length is accepted as isometrically related to size (Losey et al., 2017). Although Galeta et al. (2021) report "protodogs" to be smaller that wolves they are very large and out of the range of Pleistocene small stature dogs that have TL < 191 mm, while all Pleistocene canids have TL >225 mm and some "protodogs" even a TL of 256 mm (Janssens, Perri, et al., 2019, table 7). These specimens do not fulfill expected small size criteria. Next the statistical relative size reduction in "protodogs" in Galeta et al. (2021) is probably due to small sample size, as a much larger comparative study (n 122) could not find such difference (Janssens, Perri, et al., 2019, table 7).

It has been argued that large size of "protodogs" might have been caused by a domestication process spread over centuries or millennia (contrary to an event), and thus that size reduction was slow in developing. If so, one would expect progressively smaller specimens in time, slowly evolving to the size of generally accepted Pleistocene dogs. However, such is not the case with "protodogs", for example, Goyet, 36kya (n 1); Predmosti 27kya (n 2); Eelisevichi 15kya (n 3), in which mean TL is resp. 227 mm; 235 mm; 248 m.

It has also been argued that the onset of wolf domestication may have been partial (commensalism [Zeder, 2012]) thus inducing only minimal morphological change. Commensalism however cannot explain genetic isolation, a prerequisite for species formation. Nor has it been reported recently or historically (up to 4.3 kya; Weszeli, 2018).

Arguments above question real size difference of "protodogs" versus wolves, and indicate that the size reduction is minimal and question minimal size reduction as being caused by a slow domestication process or partial domestication.

6.2 | Viscero-cranial length

Galeta et al. (2021) measured Viscero-cranial length (VL), and referred to Morey (1992) in support. However, Morey (1992) asserted the contrary. Historically, several other studies with small population sizes also reported the VL difference (Andersone & Ozolins, 2000; Benecke, 1987; Chaix, 2000; Dimitrijević & Vuković, 2012; Harrison, 1973; Jolicoeur, 1959; Lupz, 1974; Mertens, 1936; Nehring, 1884, 1888; Okarma & Buchalczyk, 1993; Ovodov et al., 2011; Pidoplichko, Allsworth-Jones, & Djindjian, 2001; Rütimeyer, 1861). On the other hand, two large studies (one with 1700 specimens) rejected VL as species-distinguishing metric (Wayne 1984, Janssens, Perri, et al., 2019). The group separation in Galeta et al. (2021) could better be explained by normal variation which is under influence of gender or and climate-driven food stress (O'Keefe, Binder, Frost, Sadlier, & van Valkenburgh, 2014).

6.3 | Maxillary tooth row length (AL)

In Galeta et al. (2021), "Protodogs" have shorter maxilla tooth row length than Pleistocene wolves. The latter is congruent with results from an earlier mandible study (Germonpré, Láznicˇková-Galetová, Losey, Räikkönen, & Sablin, 2015) and based on nine metrics in Pleistocene canids.

We have five concerns. Two relate directly to maxillary tooth row length, three relate to mandible tooth row length. A close mandible-maxilla length connection is logical as both tooth rows are anatomically closely interlinked, thus conclusions on mandible length may probably safely be used as indirect evidence on maxillar length.

Regarding maxillary tooth row length (a) Drake et al. (2015), with a much large number of specimens (Drake et al., 2015; Table S1), failed to find dog-wolf differences in maxillary tooth row length, contradicting Galeta et al. (2021). (b) Maxillary tooth row length has been used in former studies by the same group of authors (Germonpré et al., 2009, 2012, 2017). However, in one of these (Germonpré et al., 2017) this metric did not differ between groups.

Regarding mandible tooth row length, first Brannick, O'Keefe, and Meachen (2015) showed that dire wolf mandible size-length is related to climate and not domestication. Second, Ameen et al. (2017) rejected tooth row shortening in dogs, compared to wolves (Ameen, personal communication). Third, Janssens, Perri, et al. (2019) showed that identical shorter mandible metrics could be demonstrated (using the same metrics and methodology as in Germonpré et al. (2015)) in a subgroup of German shepherd dogs, a "wolf-like" breed. Clearly, if one can subdivide such closely related specimens as German shepherds in two subgroups; one with this so-called typical domestication signature, the other groups seemingly not domesticated, it is logical to conclude that a group of Pleistocene wolf specimens, acquired from a wide geographic area and long elapsed time (see below), will vary considerably more, thus divide into subgroups more easily.

6.4 | Braincase width (GWBRC)

Braincase width was used in former studies by the same group of authors (Germonpré et al., 2009, 2012, 2017), but rarely has been used elsewhere. In two of these studies (Germonpré et al., 2012, 2017) this metric did not differ between groups. This metric was introduced by Lawrence and Bossert (1967) to distinguish between coyotes (*Canis latrans*), wolves, dogs and red wolves (*C. l. rufus*), but no difference was observed between dogs and wolves. Additionally, Pitulko and Kasparov (2017) did not confirm a difference in early Holocene dogs compared to wolves.

6.5 | Palate minimum width (MWPAL)

This metric was used by the same authors in previous studies (Germonpré et al., 2009, 2012, 2017) but was then not different between groups in two studies (Germonpré et al., 2012, 2017). We are aware of only one other study

TABLE 3 Descriptive characteristics (min., med., max., mean, *SD*) and statistical comparison (*F*-test) of seven distances on dire wolf skulls

	This study (Dire wolves)				**Galeta et al., (2020) study**	
	Cluster 1	**Cluster 2**			**Pleistocene wolves**	**"Protodogs"**
	(*N* = 24)	**(*N* = 49)**	***F* value**	***p* value**	**(*N* = 7)**	**(*N* = 8)**
Total skull length						
Min	282.25	258.6				
Median	301.55	283.85				
Max	317.51	311.08				
Mean (*SD*)	301.40 (8.23)	284.22 (11.85)	$F_{1,71} = 4.12$	$p = .0461$	*262.1 (8.31)*	*235.1 (10.2)*
Scaled effect	0.33 (0.86)	−0.16 (1.03)	Cohen's *D* = 0.52		Cohen's *D* = 2.91	
Viscerocranium length						
Min	142.25	127.6				
Median	151.53	142.2				
Max	163.09	155.97				
Mean (*SD*)	151.10 (5.32)	143.09 (6.71)	$F_{1,71} = 0.39$	$p = .5338$	*131.5 (3.78)*	*114.1 (2.48)*
Scaled effect	−0.11 (0.92)	0.05 (1.04)	Cohen's *D* = 0.16		Cohen's *D* = 5.44	
Alveolar length						
Min	94.34	87.03				
Median	101.15	96.99				
Max	108.61	106.41				
Mean (*SD*)	101.80 (3.68)	97.45 (4.20)	$F_{1,71} = 3.35$	$p = 0.0713$	*91.2 (2.46)*	*82.2 (4.61)*
Scaled effect	−0.30 (1.21)	0.15 (0.86)	Cohen's *D* = 0.43		Cohen's *D* = 2.44	
P4 mesio-distal diameter						
Min	28.22	25.21				
Median	31.4	30.16				
Max	35.81	34.51				
Mean (sd)	31.53 (1.75)	30.38 (2.05)	$F_{1,71} = 9.49$	$p = .0029$	*26.6 (1.30)*	*25.2 (1.15)*
Scaled effect	−0.49 (0.87)	0.24 (0.98)	Cohen's *D* = 0.79		Cohen's *D* = 1.10	
Greatest width brain case						
Min	59.92	58.37				
Median	65.22	71.36				
Max	79.99	86.78				
Mean (*SD*)	66.71 (5.02)	72.49 (5.74)	$F_{1,71} = 88.53$	$p < .0001$	*64.7 (2.24)*	*67.0 (3.45)*
Scaled effect	−1.06 (0.64)	0.52 (0.69)	Cohen's *D* = 2.37		Cohen's *D* = 0.79	
Greatest palatum width						
Min	105.41	96.11				
Median	113.49	114.27				
Max	125.25	126.82				
Mean (*SD*)	114.31 (5.28)	114.18 (7.25)	$F_{1,71} = 37.53$	$p < .0001$	*89.0 (3.16)*	*82.3 (5.10)*
Scaled effect	−0.83 (0.74)	0.41 (0.85)	Cohen's *D* = 1.56		Cohen's *D* = 1.58	
Smallest width palatum						
Min	43.51	39.9				
Median	51.37	50.82				

TABLE 3 (Continued)

	This study (Dire wolves)				**Galeta et al., (2020) study**	
	Cluster 1	**Cluster 2**			**Pleistocene wolves**	**“Protodogs”**
	($N = 24$)	**($N = 49$)**	***F* value**	***p* value**	**($N = 7$)**	**($N = 8$)**
Max	62.89	57.37				
Mean (sd)	51.37 (4.27)	50.23 (4.49)	$F_{1,71} = 24.72$	$p < .0001$	*47.7 (2.86)*	*46.7 (3.02)*
Scaled effect	−0.72 ± 1.09	0.35 ± 0.74	Cohen's $D = 1.15$		Cohen's $D = 0.34$	

Note: S scaled effect and effect size (Cohen's D) are also provided. For comparison with results in Galetta et al. (2020), descriptive statistics and effect sizes are also given for the skulls which they classified as Pleistocene wolves and proto dogs.

that used palate minimum width (albeit slightly differently), but found no statistical difference between (Hayonim) dogs and C.l. pallipes ($p = .26$; Tchernov & Valla, 1997; Table 3). Modern Eurasian wolves vary considerably in minimum palate width. This seems to be related to prey size, suggesting that palate minimum width is governed strongly by extrinsic influences, and would not be a useful metric for distinguishing dog from wolf (Boudadi-Maligne & Escarguel, 2014).

6.6 | Summary of validity

Only snout width is, according to us, an acceptable difference between “protodogs” and Pleistocene wolves. This one (out of seven) parameter is a weak argument to plead for domestication. Most of the differences reported by Galeta et al. (2021) could equally be explained by natural morphological variation within a population. The specimens in Galeta et al. (2021) vary considerably in deep time age (c. 34–14 kya) and geographical source region (from western Europe to Russia, >7000 km distance). Over the indicated time period, drastic climate changes strongly influenced wolf size (Aaris-Sorensen, 1977; Kurten 1965; Davis, 1981). During that same time period, this vast area included different climates that varied from quite dry in the East (modern Ukraine and Russia) to quite wet and relatively mild in the West (modern France). These extrinsic influences alone are sufficient to explain the variation seen among the specimens in the Galeta et al. (2021) study.

The fact that three metrics (AL, GWBRC, MWPAL) did not differ between groups in several former studies raised serious concerns about the robustness of these metrics. This reveals the importance of which specific specimens were selected to be examined. Such selection must have taken place as in former studies by the same authors (Germonpré et al., 2009, 2012, 2017) different, and not all, specimens were selected to be examined (Table 2).

Presenting only a selected subgroup of available specimens, as in Galeta et al. (2021), weakens, in our eyes, the strength of their argument.

7 | STUDY SIZE SAMPLE

Evaluation of earlier publications from the same group of authors (Germonpré et al., 2009, 2012, 2017) shows that nine “protodog” along with 16 Pleistocene wolf crania were reported (Table 2). Using previously studied specimens would have expanded sample size considerably Galeta et al. (2021) did not discuss their specimen selection sufficiently to help the reader understand the decision to exclude 10 previously studied specimens. The rationale behind limiting sample size would be enlightening.

8 | GENERAL CONCLUSION

We acknowledge the enormity of what we are trying to figure out when it comes to define the earliest evolutionary signals of domestication in wolves. We have less and less context the farther back in time we go, and thus our powers of resolution are vastly less. That creates uncertainties that cannot be resolved. Additionally since we were not there, and thus one must realize that much is speculative. Yet, we think that the often reported morphological differences between the so-called “protodogs” and Pleistocene wolves should be interpreted with an open mind, allowing several possible mechanisms beside domestication as evolutionary force. First, Dire wolves can be segregated into two morphological groups, including one with the same presumed domestication signature as well. That means that natural variation in a Canid population alone could also be responsible for this group division. Two, most metrics used by Galeta et al. (2021) to distinguish wolves and dogs, can be rejected, based on pre-existing work on large groups, and conflicting conclusions by the same group of authors. Three, the sizes of all specimens included by Galeta et al. (2021) miss the size reduction seen in the oldest generally accepted archaeological dogs. Four, small sample size, based on deleting previously described specimens by the same groups of authors, appears to be too small to support broad biological conclusions. We conclude that the segregation of the morphological groups (Galeta et al., 2021) easily could result from small study population size, influences of climate change, highly varied geography, long-time span, species-related evolution, variable diet, and sexual dimorphism (Munoz-Fuentes, Darimont, Wayne, Paquet, & Leonard, 2009; O'Keefe, Meachen, Fet, & Brannick, 2013) all leading to a wide normal distribution of morphological metrics. Indeed, high variability among wild wolf crania was already noted in 1884 by Nehring. Nevertheless, we cannot disprove the involvement of a domestication process either. Yet, our main message here is a cautionary one, urging for the acceptance of several alternative hypotheses or evolutionary mechanisms when interpreting morphological variation in small historical samples with little other background information.

ACKNOWLEDGMENT

We are grateful for the advice on wolf behavior by L. David Mech and the efforts from Carly Ameen to additionally examine tooth row length in her published study.

AUTHOR CONTRIBUTIONS

L A A Janssens: Conceptualization; supervision; validation; writing-original draft. **Myriam Boudadi-Maligne:** Data curation; formal analysis; methodology; validation. **Dennis Lawler:** Supervision; validation; visualization; writing-review & editing. **Robin O'Keefe:** Data curation; formal analysis; methodology; validation; writing-review & editing. **Stefan Van Dongen:** Data curation; formal analysis; methodology; writing-review & editing.

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How to cite this article: Janssens LAA, Boudadi-Maligne M, Lawler DF, O'Keefe FR, van Dongen S. Morphology-based diagnostics of "protodogs." A commentary to Galeta et al., 2021, *Anatomical Record*, 304, 42–62, doi: 10.1002/ar.24500. *Anat Rec*. 2021;1–12. https://doi.org/10.1002/ar.24624