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A landmark-based approach for assessing the reliability of mandibular tooth crowding as a marker of dog domestication

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ABSTRACT

Tooth crowding is one of several criteria used to infer the process of domestication in the zooarchaeological record. It has been primarily used to support claims of early animal domestication, perhaps most contentiously in claims for the existence of so-called "proto-domestic" dogs as early as the Middle-Upper Palaeolithic. Tooth crowding studies vary in their methodological approaches, and interpretation of the resulting data is constrained by the limited geographic and temporal scope of reference specimens used to construct an appropriate comparative framework. To address these key problems, we present a standardised landmark-based protocol for the measurement and quantification of mandibular tooth crowding that can be systematically applied in the context of dog domestication research. We then test the assumption that tooth crowding is less frequent in ancient and modern wild wolf populations by examining 750 modern dogs and 205 modern wolves from across the modern geographic range *of Canis lupus* as well as 66 Late Pleistocene wolves from Alaska.

Our results demonstrate that landmark-based metrics provide a reliable approach for recording and analysing tooth crowding. Although it is likely that the relatively low frequency of tooth crowding found in our modern dog dataset (~6%) in part reflects the 'modern' morphology of domestic breeds, the higher frequency of crowding in both modern (~18%) and ancient (~36%) wolves strongly suggests that current assumptions linking tooth crowding with the process of early domestication (at least in dogs) should be critically re-evaluated, and that further investigations into the drivers behind these developmental patterns should be pursued.

1. Introduction

A suite of phenotypic changes associated with the domestication process in mammals has been observed (and studied) in virtually all animal domesticates (e.g. Darwin, 1868; Clutton-Brock, 1999; Zeder, 2012). Traditionally, morphological changes to the skull (e.g. snout shortening, cranial flexion, and tooth size reduction; see Wayne, 1986; Clutton-Brock, 1999; Morey, 1992; Drake, 2011; Zeder, 2012), as well as size reduction of elements of the appendicular skeleton, have been the principal signature with which to track domestication in the zooarchaeological record. Another regularly accepted criterion is the presence of tooth crowding, where tooth orientation and alignment is described as touching, overlapping and/or rotated. Although there is no universally accepted definition for what constitutes a crowded toothrow, it is traditionally considered an important

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characteristic of initial domestication in dogs, (e.g. Lawrence, 1967; Clutton-Brock, 1963, 1999; Benecke, 1987; Morey, 1992; Moray, 1994; Germonpré et al., 2012, 2015a,b), and other domesticates (e.g. pigs; Krause-Kyora et al., 2013) since it is often linked with snout shortening found commonly in many domestic species. The prevalence of tooth crowding has been used as a specific criterion to identify dogs in the archaeological record (e.g. Degerbøl, 1961; Benecke, 1987; Dimitrijević and Vuković, 2012), and to support claims for the existence of Middle-Upper Palaeolithic dogs (Germonpré et al., 2012, 2015a, b; Ovodov et al., 2011).

The identification of so-called 'Palaeolithic dogs' is controversial, and researchers have suggested that additional evidence is required to support such claims (Crockford and Kuzman, 2012; Germonpré et al., 2013; Morey, 2014; Boudadi-Maligne and Escarguel, 2014; Germonpré et al., 2015a). Studies have also acknowledged that tooth crowding alone is insufficient to justify claims for the presence of early dogs (e.g. Davis and Valla, 1978; Sablin and Khlopachev, 2002; Ovodov et al., 2011). This is especially pertinent since tooth crowding has also been observed in both wild and captive wolf populations (e.g. Degerbøl, 1961; Lawrence, 1967; van Wijngaarden-Bakker, 1974; Dimitrijević and Vuković, 2012), and the natural variation of Late Pleistocene wolves remains poorly documented and not well understood (Larson et al., 2012; Crockford and Kuzman, 2012; Perri, 2016). Thus, despite its ubiquity as a proxy for domestic status, the link between tooth crowding and early domestication processes remains tenuous.

1.1. Previous methods and analyses

Previous methods for studying tooth crowding vary. In some studies, the occurrence of crowding is recorded through a visual assessment of overlapping teeth in the upper and/or lower jaw (Sablin and Khlopachev, 2002; Germonpré et al., 2012, 2015a,b; Napierala and Uerpmann, 2012). Others have developed simple biometric protocols for recording crowding using a series of ratios from length measurements of the molars and premolars (e.g. Lawrence, 1967; Davis and Valla, 1978; Benecke, 1987; Musil, 2000; Lapham, 2010; Dimitrijević and Vuković, 2012). Degerbøl (1961: 39) applied a more systematic method for measuring crowding of the maxillary toothrow as a ratio of the cumulative length of the three anterior premolars (P1, P2, P3) and the length between the canine (C1) and the carnassial (P4). Clutton-Brock (1963) later expanded this analysis to the mandible, using a ratio of the sum of the lengths of all teeth between P2 and the M3, against the total length of the toothrow measured from P2 to M3.

Degerbøl (1961) and Clutton-Brock (1963) protocols were adopted by others to assess the domestic status of canid remains from the Neolithic sites of Newgrange (Ireland: van Wijngaarden-Bakker, 1974:342), and Staines and Road Farm (England: Clark, 1996). In the case of Staines and Road Farm, measurements were limited to lower premolars only, and a new formula was defined for the maxilla *("Lengths P1 + P2 + P3) X 100/length anterior edge P1 to anterior edge P2"* — Clark 1996: 214), which differs significantly from others in terms of defining the toothrow. However, since the reported indices are largely in line with previously reported ranges (Clark, 1996: 214, table 2), it can be assumed that this definition is incorrect, and that in fact the maxillary toothrow was measured to the anterior edge of the P4 (not the P2), following Degerbøl (1961), and Clutton-Brock (1963), although only van Wijngaarden-Bakker (1974) is referenced.

These studies have produced tooth-crowding indices of continuous data that are then directly compared with other datasets, where indices of tooth crowding in wild and domestic specimens have previously been calculated (e.g. Clark, 1996; van Wijngaarden-Bakker, 1974; Walker and Frison, 1982; Ovodov et al., 2011). For instance, Ovodov et al. (2011) measured the tooth-crowding index of a 33,000-year-old canid from Razboinichya Cave (Russia) and compared it to crowding indices reported from Clark (1996) Neolithic dog samples, as well as Benecke (1994) Předmostí (Czech Republic) canid mandibles, but not with other contemporaneous specimens. The authors do, however, urge caution when using only tooth crowding as evidence for the possible presence of early domesticate dogs (Ovodov et al., 2011).

The reference datasets used as a baseline for tooth crowding in wild wolf populations are often limited both in number of specimens and geographic coverage (e.g. only modern European wolves are used in Clark, 1996). Inconsistency of the methods and metrics, as well as the development of study specific measurements (i.e. Dimitrijević and Vuković, 2012), also hinders comparisons with previously measured archaeological and wild canid specimens. Statistical analyses are additionally lacking in previous studies of tooth crowding. Although Benecke (1987) and Dimitrijević and Vuković (2012) use discriminate analysis on mandibular and maxilla measurements to study Upper Palaeolithic canids from Northern Europe and Mesolithic/Early Neolithic dogs from the Danube Gorge respectively, neither attempted to discriminate levels of tooth crowding between wild and domestic animals, even though both studies continue to note the importance of tooth crowding as an indicator of domestication (Benecke, 1987:33; Dimitrijević and Vuković, 2012).

As a result, there remains both a methodological and contextual disconnect between the recording and the interpretation of tooth crowding data. The lack of a systematic recording protocol and associated statistical methods for quantifying tooth crowding among dogs and wolves means the overriding hypothesis that crowding is a product of domestication has yet to be empirically tested on appropriate modern wild and domestic comparative material.

To address this, we refined and adapted the methods of Degerbøl (1961) and Clutton-Brock (1963) for recording mandibular tooth crowding using easily applicable landmark-based approaches. We then applied these protocols to a large sample of modern/recent domestic dog and wolf mandibles, along with a sample of Pleistocene wolves. We first tested which (if any) group showed the highest proportion of specimens with tooth crowding, as well as which group contained specimens with the highest overall crowding value. We then tested whether instances of tooth crowding differed between wolves and dogs, and whether it was possible from these data to distinguish wolves and dogs based on these measures of tooth crowding.

2. Materials

A total of 1021 specimens were analysed, including 750 modern domestic dogs, 205 modern Grey wolves (*Canis lupus*), and 66 Pleistocene wolves. The modern dog sample derived from the collection at the Natural History Museum of Bern (Switzerland) and consists of pure bred individuals collected or donated to the museum since the early 20th century. The late Pleistocene wolves are all from Alaska, USA (housed in the American Museum of Natural History), 14 of which have been directly dated to between 45,500 ± 2700 uncal BP to 15,268 ± 169 uncal BP (Leonard et al., 2007 & Supplementary Information; also SI 2, SI Fig. 2 this paper). The modern wolf specimens cover the full extent of *Canis lupus*' natural range in both North America and Eurasia (Fig. 1). These modern wolves came from collections held at the Smithsonian Institute (Washington DC), Lisbon Natural History Museum,