Archaeophenomics of ancient domestic plants and animals using geometric morphometrics : a review

Allowen Evin[1], Laurent Bouby[1], Vincent Bonhomme[1], Angèle Jeanty[1], Marine Jeanjean[1], Jean-Frédéric Terral[1]

[1] ISEM, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France. 2 place Eugène Bataillon, 34095 Montpellier, cedex 5, France.

Orcid numbers:

Allowen Evin: 0000-0003-4515-1649
Laurent Bouby: 0000-0002-3633-9829
Vincent Bonhomme: 0000-0002-2742-6349
Angèle Jeanty: 0000-0002-0673-0704
Marine Jeanjean: 0000-0001-5407-509X
Jean-Frédéric Terral: 0000-0003-1921-2161

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Abstract

Geometric morphometrics revolutionized domestication studies through the precise quantification of the phenotype of ancient plant and animal remains. Geometric morphometrics allow for an increasingly detailed understanding of the past agrobiodiversity and our ability to characterize large scale ancient phenotypes has led to what can be named archaeophenomics : the large scale phenotyping of ancient remains. This review describes advances in the bioarchaeological study of domesticated species and their wild relatives where their phenomes are quantified through geometric morphometrics. The two main questions addressed by archaeophenomics are i) taxonomic identification, including domestication signature, and ii) the inference of the spatio-temporal agrobiodiversity dynamics. Archaeophenomics is a growing field in bioarchaeology of domestic species that will benefit in the near future from advances in artificial intelligence and from an increasing interest in multiproxy approaches combining morphometric data with *e.g.* isotopes or archaeogenomics.

1. Introduction

Domesticated species have played a major role in the development of Charles Darwin's work, being the subject of the first chapter of the 'Origin of Species' (Darwin, 1859) and later of a dedicated book, 'The variation of animals and plants under domestication'(Darwin, 1868) where he described the mechanisms of variation in domestic species. With his work, Darwin contributed to the understanding of the morphological changes that occurred during the long process of domestication. For most domesticated species, modern breeds and varieties today present a huge morphological diversity reflecting millennia of human selection for many purposes (*e.g.* food production, work, aestheticism) in various environmental conditions. While the study of the current domestic diversity is mainly carried out in agronomic research, with breed and varietal improvement using molecular breeding programs, a large amount of research has been done to explore the past diversity of domestic species whose remains are found in increasing numbers in archaeological deposits. The methodological development in morphometrics have revolutionized, qualitatively and quantitively, the study of the phenotype of those remains. Today we have reached a state where the use of several tools, including morphometrics, have allowed phenome (*i.e.* the full set of observable traits) quantification of a large number of archaeological specimens leading to a renew in the study of archaeological remains of domestic species. We here coin the word *archaeophenomics* for such large-scale quantification of phenotypic data from archaeological specimens. Archaeophenomics, *i.e.* phenomics of the past, is an emerging field that will likely become a standard for future bioarchaeological studies. This neologism fulfils the needs to express the new realities of bioarchaeological domestication studies.

From phenomics to archaeophenomics

Phenomics, the analysis of high-dimensional phenotypic data, is part of the '-omics' revolution as genomics or proteomics. Phenomics is the new generation of acquisition and analysis of phenotypic data based on techniques which allow a very large amount of quantitative characters to be acquired and processed with minimal handling time. Assessing the full phenome of an organism is illusional (Houle, Govindaraju, & Omholt, 2010) and this is even more true in bioarchaeology. Archaeological remains of plants and animals are often altered by taphonomical processes (*e.g.* preservation, fragmentation). Despite these inherent constraints associated with studying archaeological material, the large quantity of remains allows for large-scale morphometric analyses.

Morphometrics is one of the many tools of *phenomics.* The 'morphometric revolution' corresponding to the development of *geometric morphometrics* (GMM), *i.e.* the study of forms in multi-dimensional spaces, allow more in-depth investigation of morphological changes (Adams, Rohlf, & Slice, 2004; Rohlf & Marcus, 1993). The main improvement of geometric morphometrics compared to the so-called 'traditional morphometrics' is that biological forms are no longer captured by sets of independent measurements of lengths or angles, but by sets of point coordinates, improving dramatically the capture of the geometric complexity of these objects (Bookstein, 1991; Kuhl & Giardina, 1982; Rohlf & Marcus, 1993). Morphometric analyses are often the only available approach for studying the morphology of ancient remains with a fine-scale resolution, while suffering less from preservation limitations than *e.g.* ancient DNA and offering much better possibilities for being carried out on a large scale at a limited cost, in both time and money. This is especially true for plants whose remains are often found charred, a condition strongly detrimental to DNA preservation and which generally prevents the analysis of these remains, at least with current aDNA techniques (Nistelberger, Smith, Wales, Star, & Boessenkool, 2016). Most of the time, once a specimen is recovered a morphometric analysis can be performed, as long as the structures grabbing the geometrical features analysed are present. While it is always better to analyse complete specimens, fragmented remains can even be studied using a restricted version of the initial protocol since fragmentation does not necessary prevent taxonomical identification (e.g. Cornette et al., 2015; Owen et al., 2014, Durocher in press). Geometric morphometric techniques are therefore particularly well adapted to bioarchaeological studies and are a growing field in the discipline.

Archaeophenomics appears to be as a major breakthrough in bioarchaeology, with a drastic quantitative change in the scale of the number of specimens and populations that can be analysed, and a qualitative improvement provided by an increased resolution of the analyses paired with a better description of the morphometric variation with improved detection and visualisation of the shape variation.

Aim and scope of the review

Here we provide an exhaustive review of bioarchaeological studies using archaeophenomics, through geometric morphometrics, to study archaeological remains of domestic species. We restricted our review to studies published in international journals (*i.e.* excluding grey literature), only those focusing on domestic species and that include archaeological specimens.

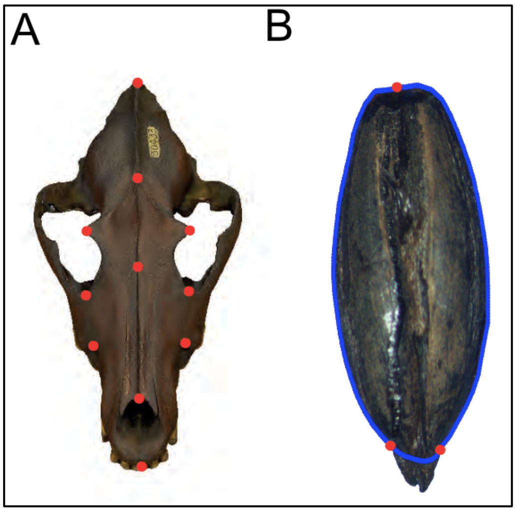
This therefore explicitly excludes: studies of commensal species (*e.g.* rodents (Cucchi, 2008; Cucchi et al., 2014; Valenzuela-Lamas, Baylac, Cucchi, & Vigne, 2011)); studies focusing only on the ancestors and modern relatives of the domestic populations (*e.g.* Late Glacial horse (Bignon, Baylac, Vigne, & Eisenmann, 2005), rabbit (Pelletier, 2019)); and finally the numerous studies focusing only on modern domestic specimens (*e.g.* Battesti et al., 2018; Bonhomme et al., 2017; Evin et al., 2022; Evin, Dobney, et al., 2015; Gros-Balthazard et al., 2016; Hanot et al., 2021; Harbers et al., 2020; Neaux et al., 2020; Pelletier, Kotiaho, Niinimäki, & Salmi, 2020, 2021). Yet these studies are of prime interest for the understanding of ancient populations, they fall out of the scope of this review.

2. Geometric morphometrics in archaeophenomics

The development of geometric modern morphometrics (GMM) (Bookstein, 1991; Rohlf & Marcus, 1993) came as a response to the conceptual and methodological limits of traditional morphometric methods, such as a better ability to efficiently partition the size and the shape components of the form variation and the possibility of visualizing shape variation. Shape analysis, through geometric morphometrics, allows analysing microscale variation that could not otherwise be identified using traditional techniques. Two main geometric morphometric approaches are currently used in bioarchaeology (fig. 1): **Procrustes approaches** through the acquisition of landmarks and sliding semi-landmark coordinates **and outline analyses** using various methodologies (see below). In bioarchaeology, as in biology, objects are studied in two- or three-dimensions depending on the geometry and size of the remains. Until recently, all archaeobotanical remains appear to have been studied in 2D from digital images, though one recent publication used 3D X-ray-computed tomography to quantify watermelon seeds (Wolcott et al., 2021) (table 1). In addition, archaeobotanical remains are nearly exclusively studied through their outlines geometries using mainly either Elliptic Fourier transforms (EFT) (Giardina & Kuhl, 1977; Kuhl & Giardina, 1982) or natural/orthogonal polynomial equations (Rohlf, 1990) (table 1) and only few studies use landmarks and sliding semi-landmarks coordinates (Ros et al. 2014; García-Granero et al. 2016; Wolcott et al. 2021) (table 1).
For animals, teeth are studied in 2D and the same applies to some postcranial bones (*e.g.* phalanges, and talus) although it is quite possible to study them in 3D (Hanot, Guintard, Lepetz, & Cornette, 2017; Haruda, 2017) (table 1). The same applies to mandible that are studied either in 2D (cat: (Vigne et al., 2016), dog: (Ameen et al., 2019)) or 3D (dog: (Drake et al., 2017)).

Skulls, which are geometrically more complex objects, are studied in 3D, either directly on the specimens using *e.g.* a Microscribe digitizer (Drake & Klingenberg, 2008; Geiger et al., 2017; Hanot et al., 2017) or through 3D model reconstruction obtained by CT-scanning (Schoenebeck, Hamilton-Dyer, Baxter, Schwarz, & Nussbaumer, 2021) or photogrammetry (dog: (Ameen et al., 2019)). So far, a single study really takes advantage of a CT-scanning technology to analyze the internal structure of the skull that is the inner ear morphometry (Clavel et al., 2021).

<Figure 1> Example of geometric morphometric protocols applied to bioarchaeological remains. A Example of Procruste approaches used to quantify the morphometric variation of canid skulls with 3D landmarks. B Example of protocols for 2D outline analyses used to quantified the morphometric variation of barley grains.



3. **Domestic species studied with geometric morphometrics**

We identified a total of 71 studies among which 38 focus on animals and 33 on plants (fig. 2.A, table 1, SI table 1).

For animals, only mammals have been studied (though a PhD thesis should be mentioned on chicken (Foster, 2018)), which also represent the large majority of domesticated animals. Ten species are listed and the most represented taxa are pig (N=16), followed by dog (N=9), equids (N=5, horse and donkey), caprines (sheep and goat) (N=5), camelids (N=3, guanaco and llama), and finally cat, and cattle with a single mention (table 1, fig. 2). Animal studies focus primarily on teeth (N=21), skull (N=10, cranium and mandible), in a much larger majority than postcranial bones (*e.g.* talus, phalanges or calcaneus) (SI-table 1).

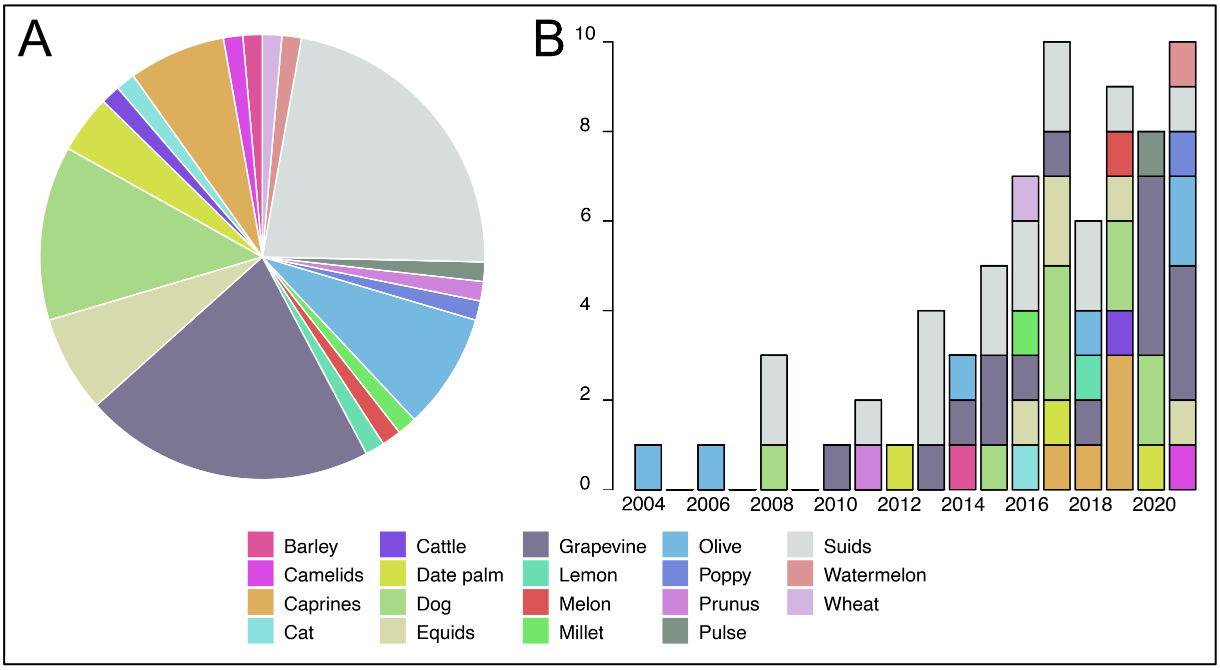
For plants, only angiosperms are concerned and 14 species (or group of closely related species) are listed with grapevine that largely outnumber other species in terms of publications number (N=15), followed by olive (N=6), date palm (N=3) while all other species are only represented by a single mention (table 1). A higher number of studies is dedicated to dicotyledons (N=27) than to monocotyledons (N=6) and focus exclusively on fruits and seeds (SI table 1).

<Table 1> List of the reviewed publications. An extended version of the table, including research themes, employed methodology, and combination with biomolecular markers can be found in SI-table 1.

Group	Taxa	References
Mammals	Pig	(Balasse et al., 2016; Bartosiewicz et al., 2013; Bopp-Ito, Cucchi, Evin, Stopp, & Schibler, 2018; Cucchi et al., 2016, 2021; Cucchi, Fujita, & Dobney, 2008; Cucchi, Hulme-Beaman, Yuan, & Dobney, 2011; Dobney, Cucchi, & Larson, 2008; Duval, Cucchi, Horard-Herbin, & Lepetz, 2018; Duval, Lepetz, Horard-Herbin, & Cucchi, 2015; Evin, Flink, et al., 2015; Frémondeau, De Cupere, Evin, & Van Neer, 2017; Krause-Kyora et al., 2013; Marom et al., 2019; Ottoni et al., 2013; Price & Evin, 2017)
	Dog	(Ameen et al., 2019; Daza Perea, 2017; Drake, Coquerelle, & Colombeau, 2015; Drake et al., 2017; Drake & Klingenberg, 2008; Fisher, 2019; Geiger et al., 2017; Manin & Evin, 2020; Schoenebeck et al., 2021)
	Caprines (sheep and goat)	(Colominas et al., 2019; Haruda, 2017; Haruda, Varfolomeev, Goriachev, Yermolayeva, & Outram, 2019; Pöllath, Alibert, Schafberg, & Peters, 2018; Pöllath, Schafberg, & Peters, 2019)
	Equids (horse and donkey)	(Chuang & Bonhomme, 2019; Clavel et al., 2021; Cucchi et al., 2017; Hanot et al., 2017; Seetah, Cardini, & Barker, 2016)
	Camelids (guanaco and llama)	(Hernández, L'Heureux, & Leoni, 2021)
	Cat	(Vigne et al., 2016)
	Cattle	(Cucchi et al., 2019)
Monocotyledons	Date palm	(Gros-Balthazard et al., 2017; Sallon et al., 2020; Terral et al., 2012)
	Barley	(Jérome Ros, Evin, Bouby, & Ruas, 2014)
	Millet	(García-Granero et al., 2016)
	Wheat	(Bonhomme et al., 2016)
Dicotyledons	Lemon	(Grasso, Mavelli, & Fiorentino, 2018)
	Melon	(Sabato et al., 2019)
	Grapevine	(Bacilieri et al., 2017; Bonhomme et al., 2020; Bonhomme, Terral, et al., 2021; Bouby et al., 2018, 2021; Figueiral et al., 2015; Mariotti Lippi et al., 2020; Margaritis et al., 2021; Moricca et al., 2021; Orrù, Grillo, Lovicu, Venora, & Bacchetta, 2013; Pagnoux et al., 2015, 2021; Terral et al., 2010; Ucchesu et al., 2015, 2016; Valamoti et al., 2020)
	Olive	(Bourgeon et al., 2018; Margaritis et al., 2021; Newton, Lorre, Sauvage, Ivorra, & Terral, 2014; Newton, Terral, & Ivorra, 2006; Terral et al., 2004, 2021)
	Opium poppy	(Jesus et al., 2021)
	Cherry	(Burger, Terral, Ruas, Ivorra, & Picq, 2011)
	Pulses (grass pea, lentil, broad bean)	(Tarongi et al., 2020)
	Watermelon	(Wolcott et al., 2021)

Since 2004, year of the first publication included in this review (Terral et al., 2004), the yearly number of published bioarchaeological studies on domestic animal and plant species using geometric morphometrics is steadily increasing (Fig. 1.B).

<Figure 2> Bioarchaeological archaeophenomic studies, concerning domestic species and using geometric morphometrics, represented by taxa (A) and year (B). A: relative frequencies of the different groups studied. B: Evolution of the number of studies per year. Details of the references can be found in table 1 and SI table 1.



The number of phenomes now available greatly differs between species with grapevine coming out on top with a maximum of 2223 archaeological seeds having been quantified in one single study (Pagnoux et al., 2021). The number of papers published per year is still low compared to *e.g.* palaeogenomic studies (~1480 references obtained for a quick online search of the term "palaeogenomics" in google scholar the 11/02/2022). Numbers of studied individuals are usually lower for animals which are mostly represented by fewer individuals per archaeological assemblage. It should be noted, however, that the concept of 'individual' differs here between archaeozoology and archaeobotany, since an animal will be represented by single elements such as a cranium or a lower right third molar, while numerous studied individuals (*e.g.* seeds or fruit-stones) may come from a single plant individual.

4. Main bioarchaeological research themes based on GMM data

Archaeophenomics through geometric morphometrics is increasingly used for bio-archaeological studies for two main purposes that are the **taxonomic identification** of the archaeological remains including the domestication signature, and to assess the **agrobiodiversity variation in both time and space** primarily related to processes of colonisation-dispersal, adaptation, diversification and changes in husbandry or cultivation practices or cultural choices.

Taxonomic identification and domestication signature

A prerequisite of many bioarchaeological studies is to perform a taxonomical identification of the remains, either by identifying the taxa to which the specimen belongs and/or to identify its wild or domestic status. Archaeological remains are often fragmented or altered due to either taphonomic due to various anthropic and taphonomic processes (*e.g.* charring. butchery or culinary preparation) processes rendering their identification potentially delicate. Geometric morphometric protocols are now available to distinguish (more or less effectively depending on the study and model) morphologically close mammalian species of equids, bovids, sheep-goats, camelids, canids, cats and pigs (table 1). Taxonomic identification of plant remains is even more challenging due to the larger number of species (or sub-species) potentially occurring at an archaeological site. Botanical studies dealing with taxonomic identification include cereals, such as barley, millet, einkorn and emmer, opium poppy, pulses, citrus, melon, watermelon, date palm and prunus species (SI table 1). For other remains whose species identification is unambiguous, the question of the wild and domestic status distinction and identification may arise. This is especially true for species that have a wild ancestor with a wide geographical range and for which the wild and domestic populations have coexisted for millennia. This is the case for nearly all species with the exception of those having an ancestor leaving in a restricted geographic area (*e.g.* sheep, goat and most cereals). This geographic proximity can also be source of hybridization between wild and domestic individuals as already documented from genomic and palaeogenomic data*.* for *e.g.* pig (Frantz et al., 2019), dog (Pilot et al., 2018), grapevine (Myles et al., 2011; Riaz et al., 2018) or date palm (Gros-Balthazard et al., 2017) or among individuals of distinct species as evidenced for north African date palm (Flowers et al., 2019) which can render their morphometric identification even more challenging. In addition, studies looking at bridging archaeological samples to modern breeds or varieties, or groups of them, are more often found for perennial clonal plants, that show an extended varietal diversity and for which varieties can theoretically persist substantially unchanged for centuries or even millennia through vegetative multiplication (*e.g.* grapevine, olive, *Prunus* species and date palm (table 1)). For non-perennial clonal organisms, such as animals, it seems that direct comparison to specific modern breeds has been done, so far, only for dogs (Geiger et al., 2017; Schoenebeck et al., 2021), and that such comparison can be questioned as the intensification of selective pressures during the last centuries likely dramatically altered ancient morphologies.

Another specificity of archaeobotanical remains compared to zooarchaeological ones is that remains are often found charred and that charring can affect their size and shape and therefore their taxonomic identification. An important effort has been made for multiple taxa to understand the effect of charring on the morphometric results and their interpretations (*e.g.* cereals (Bonhomme et al., 2017; Ros et al., 2014), grapevine (Bouby et al., 2018; Ucchesu et al., 2016), and olive (Terral et al., 2004)).

A significant proportion of the domestic species whose remains are found during archaeological excavations have been the subject of geometric morphometrics and such approaches have been found effective for taxonomic identification of the remains. The many available protocols can now be adapted to nearby species not yet subjected to such studies.

Documenting spatio-temporal variation of past agrobiodiversity

A large number of archaeophenomic studies explore the morphometric spatio-temporal variation of domestic populations. Such studies span either long periods of time of several millennia (*e.g.* Pagnoux et al., 2021; Price & Evin, 2017; Terral et al., 2004), or a much shorter period of no more than a century (*e.g.* Drake & Klingenberg, 2008).

Time and space are intertwined components of bioarchaeological studies. It is however possible to study them separately by comparing either diachronic populations of a single locality or synchronous populations of various geographic origins.

The studies that explore the geographic variation between populations from a single chrono-cultural period (SI-table 1) evidenced that both geographically near and far populations can show morphometric differences. In term of interpretations, a geographic structuration of synchronous populations may correspond not exclusively to local environmental adaptation, different husbandry/cultivation practices, cultural choices or distinct genetic lineages.

Similarly, diachronic differences between populations originating from the same geographic area can reveal either changes in human practices, spread of new genetic stock, environmental variation, or drift. Such comparison between diachronic populations (SI-table 1) can reveal both long term variation, but also more abrupt morphological shift between periods.

In comparison, fewer studies focus both on time and space (SI-Table 1). Generally, while absence of differences between assemblages cannot lead to the conclusion that they belong to similar populations, on the other hand, the existence of differences allows to hypothesize the existence of distinct populations with at least limited cultural or genetic exchanges. As a consequence, morphometric analyses can make only limited contribution to mobility studies, that can be better explored using *e.g.* biomolecular markers such as ancient DNA or isotopes. In the same way, phenotypic proximity does not necessarily reflect genetic proximity (*i.e.* phylogeny) due to natural or anthropic selection. During domestication, human populations have selected certain traits such as larger quantity of meat or of fruit size. In archaeophenomics studies, the target of human selection during domestication and subsequent diversification is not necessarily the target of the morphometric analysis. For cereals, grain size was likely intentionally selected, but not their shape, while for fruit stones neither size or shape were likely directly targeted, even if in some cases (*e.g.* at least for grapevine) seed and fruit measurements covariate (Bonhomme et al., 2020). Similarly, in mammals, it is unlikely that teeth, that are commonly studied and considered as a phenotypic marker of adaptation to natural or anthropic environment, were not likely the aim of human selection that primarily targeted primary (*e.g.* meat) or secondary products (*e.g.* milk, wool). In all these cases, where domestic and wild populations differ in size and shape of anatomical elements non targeted by selection, other evolutionary pressures and mechanisms such as drift, genetic hitchhiking or indirect selection (*e.g.* morpho-functional constraint) can be invoked. In addition, many anatomical structures are polygenic (*e.g.* Harjunmaa et al., 2012), or the genes involved are not known. Moreover, not all anatomical elements necessarily evolve in parallel, at the same rate or following the same direction (*e.g.* Geiger & Sánchez-Villagra, 2018).

5. Multi-proxy approaches and future methodological developments

Archaeobotanical remains are often conserved through charring which is detrimental to DNA preservation (Nistelberger et al., 2016) rendering the combination of such approaches with morphometric data impossible. This is however possible to the less frequently found waterlogged remains where DNA can be preserved and the results compared to morphometric data (Bacilieri et al., 2017; Bouby et al., 2021).

For animals, several studies combined geometric morphometrics with ancient DNA (*e.g.* pig: (Evin, Flink, et al. 2015), dog (Ameen et al., 2019)), geometric morphometrics and isotopes (pig: (Cucchi et al., 2016; Frémondeau et al., 2017)), or the combination of the three approaches geometric morphometrics, ancient DNA and isotopes (pig: (Balasse et al., 2016)). Isotopic analyses are increasingly used in archaeobotany (*e.g.* Fiorentino, Ferrio, Bogaard, Araus, & Riehl, 2015), but not yet in combination with other approaches.

Artificial intelligence is increasingly used in biology (*e.g.* Ching et al., 2018; Hassoun et al., 2021) and archaeology (*e.g.* Bickler, 2021; Horn et al., 2021), but only few bioarchaeological studies use yet such approaches (*e.g.* Miele, Dussert, Cucchi, & Renaud, 2020). Machine learning in general, and deep learning using convolutional neural networks in particular, will certainly help in the future for automatic data acquisition such as landmark coordinates (*e.g.* Devine et al., 2020), image post-treatment prior to outline analyses, and/or directly for binary (status) or multiple (species identification) classification tasks. In addition, the ever-growing motivation to share data and knowledge should drastically extent the chrono-cultural and geographic scopes of the studies allowing comparisons not possible before. This would be possible only after careful inter-operator and methodological comparisons (Evin, Bonhomme, and Claude 2021). Other future lines of research will also certainly focus on evo-devo perspectives (Bonhomme et al., 2020), form-function interactions (Harbers et al., 2020; Neaux et al., 2020) as well as further exploration of the genotype-phenotype relationships (Schoenebeck & Ostrander, 2013).

6. Conclusion/perspectives

Archaeophenomics through geometric morphometrics allows addressing questions regarding the micro-evolutionary processes that accompanied the long history of domestic species in an unprecedented way. Such approaches are increasingly used in bioarchaeology and are becoming one of the many approaches now available to us to study past populations. The future of phenotypic studies will require carefully thought, managed and open large-scale databases, precisely contextualised archaeologically, and combining the whole set of available approaches, if possible carried out on the exact same specimens. As for the relatively recent research fields of palaeoproteomics or palaeogenomics, this review shows that archaeophenomics definitely corresponds to a renew of domestication studies deserving a new terminology. This review attempts to list all the studies in the scope of archaeophenomics where the phenomes of domestic species are quantified through geometric morphometrics. The many approaches now available pave the way to future research expanding the diversity of studied species and the archaeological questions that can be addressed through archaeophenomics.

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Conflict of interest disclosure

The authors declare they have no conflict of interest relating to the content of this article.

Supplementary information

SI-Table 1 is available in the open repository OSF with the DOI : 10.17605/OSF.IO/T3Q96.

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