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Introduction

Neanderthals: Ecology and evolution

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In one of the last scenes of a legendary movie, *The Last Samurai*, Captain Algren (played by Tom Cruise) appears on his knees in the presence of the Emperor Meiji (played by Shichinosuke Nakamura). The Emperor asks Algren about the great Samurai hero Katsumoto (played by Ken Watanabe) and the dialogue transpires as follows:

- Emperor Meiji: *The Samurai is gone. The spirit of samurai lives forever. Tell me how he died.*
- Captain Algren: *I will tell you how he lived.*

We hope not to have been excessively heterodox with this initial artistic license that aims to summarize the philosophy that transcends this special volume. Rivers of ink have been shed on Neanderthal extinction and also on their supposed cognitive disabilities and behavioral differences with our own species. This special issue will not focus on the demise of the Neanderthals, but instead on their long history and ecological environments. On how Neanderthals lived. The volume focuses on aspects of the origins of Neanderthals, their evolution, their ethology and also their disappearance as a fossil entity. The latter does not signify the genetic extinction of the species, because the Neanderthal endures in many of us. It is also clear that the debate on Neanderthal extinction includes tendencies in the scientific literature that have little to do with the evidence and much with the weight of tradition or perhaps the prestige of the authors and/or journals. In this context, the chronology has become a kind of new idol; but a date is only a date and one can not ignore all the ecological, anthropological, social and cultural perspectives. This collection of papers also has a goal of offering a certain balance between papers that seek and propose general trends and others that focus on more particular

stories, on deterministic and historical contingency approaches (see Fig. 1).

Carrión and Walker (2019) provide a background to Neanderthal presence in Western Mediterranean Europe. Habitual tool-use underpinned human survival in late Early Pleistocene western Mediterranean Europe. In the beginning of the Middle Pleistocene, humans were exploiting diverse biotopes, attaining primary access to large game, and deploying a variety of stone artifacts, which implies not only manual dexterity but also technical competence and cognitive versatility. Late Early Pleistocene human behaviour foreshadowed that of Middle Pleistocene pre-Neanderthal humans whose background conceivably had deep regional roots. By the mid-Middle Pleistocene *Homo heidelbergensis* was exploiting a wide range of natural resources in western Mediterranean environments, including small game and plants. Neanderthal morphology seems to have emerged during the second half of the Middle Pleistocene, accompanied by increasing technological diversity and an expanding variety of small tools, conjecturally used for by hafting, perhaps following the development of wooden spears (or other tools) and adhesive and binding technologies, as well as the generation and heat-control of fire. By the onset of the last interglacial period, Neanderthal morphology and Mousterian artifacts are widespread, and there are indications of coordinated retrieval and treatment of body-parts of large ungulates.

The tempo and mode of Neanderthal evolution is the bone of contention for Rosas et al. (2019) who perform a geometric morphometric comparative analysis of the Mauer, Arago and Atapuerca-SH specimens craniofacial osteology. As a part of the craniofacial system, the mandible is used as a study model because of its iterated occurrence in the fossil record, and the fact that it contains diagnostic features related to its sensitivity to developmental factors. Rosas et al. (2019) observe that the three specimens analysed can be considered members of the Neanderthal lineage, which may therefore be traced back to at least 0.6 million years. A

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Fig. 1. Location of the sites mentioned in this paper.

major connotation is that there would be only one polytypic species of *Homo* in the Middle Pleistocene of Europe. This is quite a structuralist approach (against populational-based interpretations) for interpretation of the European Middle Pleistocene hominin diversity. In particular, the pattern of variation in the vertical configuration of the face, which is based on well-differentiated growth patterns and is shared by hominids, is here regarded to be the structural factor that explains the variation detected within and between the European Middle Pleistocene samples.

Certainly, the patterns of morphological variation in the hominin fossil record of the European Middle Pleistocene are a useful tool for testing a diversity of taxonomic and evolutionary hypotheses. Like the mandible, tooth morphology can be considered to be highly heritable, selectively neutral, and evolutionarily conservative, thus providing an excellent proxy for neutral genetic data (Scott and Turner, 1997). In this issue, Bermúdez de Castro et al. (2019) carry out a metric and morphological comparative study of dental samples from Arago and Sima de los Huesos. The geographic proximity of these sites must be taken into account, as well as the fact the samples studied are approximately the same age. Whereas the Sima de los Huesos teeth show typical Neanderthal features, the Arago specimens exhibit a combination of plesiomorphic together with Neanderthal-derived features. The authors discuss these data in the framework of Eurasian hominin evolution postulating that Europe was settled at different points in time by groups coming from southwestern Asia, from which successive waves of populations may have been displacing westwards. The pioneer settlers might be the plesiomorphic morphotypes, and the most recent settlers would be more like typical Neanderthals. A biogeographic and evolutionary picture is depicted involving events of geographic isolation, genetic drift, directional adaptation,

and hybridization.

The puzzling panorama of morphological characteristics among pre-Neanderthals and Neanderthals appears to be the outcome of the aforementioned myriad of interacting mechanisms. Some bone-specific studies are worth discussing because of their evolutionary signification. Di Vincenzo et al. (2019) bring to light the scapula of the Altamura Neanderthal (Puglia, Italy) dated to a late Middle Pleistocene bracketed between 128.2 and 187.0 ka. Morphological analyses show that this bone falls within the range of Neanderthal variability, resembling the Mid-Pleistocene sample from Atapuerca Sima de los Huesos. However, this scapula exhibits a bisulcate/ventral pattern of the axillary border, a detail that is uncommon among Neanderthals. The scapula from Altamura is thereafter used by Di Vincenzo et al. (2019) to review the cranial variability along the Neanderthal lineage. This paper highlights the importance of even a single bone in order to investigate evolutionary patterns of morphological variation in Neanderthals.

Another outstanding contribution in the anatomical morphological story line is conducted by Jiménez et al. (2019) on the frontal bone of the specimen CE-05877 from Carihuela Cave, southern Spain. These authors implement a virtual reconstruction of this bone's three-dimensional morphology through geometric morphometric analyses, showing it falls within the range of shape variation of 6–7 year-old Neanderthals, and clearly outside the range of variation exhibited by same-age modern humans. This study reinforces the view that Neanderthals and modern humans retain recognizable frontal bone morphologies, while their cerebral frontal lobes exhibit largely similar but highly variable sulcal patterns. Hence, Jiménez et al. (2019) confirm disparities reported previously in frontal bone morphology (e.g. Gunz and Bulygina,

2012), which might be already present at birth (Ponce de León et al., 2016). Plausibly during postnatal development, these differences would become more prominent in connection with more intense facial growth in Neanderthals. Unquestionably, anatomical differences between both species may be conspicuous, as a recent study by Gunz et al. (2019) has emphasised. Above all, indices of endocranial shapes demonstrate that our braincase is more spherical than that of Neanderthals. Indeed, this appears to be another demonstration of neoteny in modern humans.

The taphonomy of skeletal finds can provide interesting information on Neanderthal life. Fernandez-Jalvo and Andrews (2019) develop a taphonomical analysis of *peri-mortem* traumas in Neanderthal remains from Spy Cave at Belgium. These remains have been influential to the concept of the species as archaic fossil humans in relation to modern human populations. These authors investigate the cause of death of two individuals, and why they occurred at this site, specifically whether they were buried. Several hypotheses are discussed, from human cannibalism to intentional funerary burials. Some of the conclusions are (i) that the Spy faunal remains were broken and butchered by contemporaneous hominins, although it cannot be corroborated that these hominins included Spy I/Spy II, or that the Spy Neanderthals were living in the cave; (ii) that the two individuals were not cannibalized; (iii) that intentional burial should be excluded. It can also be conjectured that both Spy I and Spy II were killed by blows to the top and front of the head at time of death. Forensic criteria distinguishing between crime or fall of these individuals, supports interpersonal violence and intentional blows for the Spy I and Spy II individuals.

While being a thought-provoking research case, the above conclusions should not mislead us. The general evidence is that Neanderthals are far from being the ruthless brutes that paleoanthropology first concluded. This is the scenario of Spikins et al. (2019)'s paper, which deals with healthcare practices amongst Neanderthals. They propose fossil evidence for the survival from severe illness and injury, and a long list of examples from pathology in Neanderthal skeletal material suggesting healthcare. Surely, care for the ill and injured must have had a long evolutionary history and to have been crucial in improving health and reducing mortality risks. Hypothetically, healthcare in Neanderthals would have been selectively favoured by the intrinsically stressful environments with high injury risks at the time. At the very fringes of the North Temperate Zone, this strategy may have been of paramount importance.

Spikins et al. (2019) major work also provides explanatory power to the ecology and evolution of other hominins because healthcare provisioning must have functioned to mitigate risks in any highly collaborative and interdependent group. The approach of this article is quite different from the literature on Neanderthal adaptive contexts. While it is clear that much adaptive success depends on skills in hunting, shelter, fire or clothing, much less discussion exists on the eco-evolutionary implications of reducing mortality risks through the provision of medical care. This is especially true in biotopes that were likely to be located in climatically hostile regions, many of which were occupied by Neanderthals for long periods of time. Yet, these environments are not preferentially occupied, as we shall see.

Stewart et al. (2019) put into question the long standing view that Neanderthal anatomy is an adaptive feature of cold environments by instead testing an alternative hypothesis, that they were specialised hunters of woodlands which necessitated a rapid turn of speed. The idea that they were woodland hunters had been suggested before by various authors over the years (Stewart, 2004; Finlayson and Carrión, 2007) but the idea that their anatomy, with powerful musculature was due to a capacity for sprinting has been

little considered. The hypothesis was explored in relation to the palaeoecology of their most northern limits during MIS3 and tested using an analysis of their genetics. Both these sources of data were consistent with the hypothesis. This paper also reexamines the ecological associations of Neanderthals at one of the more important sites in North West Europe – Walou Cave, Belgium. Also included are the use of the genetics of collared lemmings in Belgium to examine the palaeoecology of the area during MIS 3, proposing that *Dicrostonyx torquatus* may not have been coeval with Neanderthals as one seemed to preferentially live during the interstadials (the Neanderthals) while the other underwent population turnovers at those interstadials (the collared lemmings). These two mammal species may have been the most cold-adapted and warm adapted taxa of North Western Europe during MIS3 and hence cause one to question the most extreme components of the steppe tundra of the late Pleistocene. This may cause one to question the so called non-analogue environment of MIS 3 previously considered to be such an important characteristic of the time (Stewart, 2005).

New data from excavation campaigns are welcomed. Spagnolo et al. (2019) visit the Stratigraphic Unit 13 of the Oscuruscio Rockshelter (Ginosa, Taranto, Southern Italy), which is a Mousterian palimpsest representing the first stable occupation of the site soon after the deposition of a thick layer of tephra (Mt. Epomeo Green Tuff - Ischia datable to around 55 kya BP). The authors present multidisciplinary research with an integrated method that includes lithics, fauna, and microarchaeology of combustion features. They eventually suggest the occurrence of a tripartite location made of spatially segregated and integrated activity areas. This study is important for the progress in understanding Neanderthal subsistence strategies and intra-site spatial management.

Moroni et al. (2019)'s paper focuses on the chronology, geo- and zooarchaeology of Grotta dei Santi in Monte Argentario, southern coast of Tuscany. The sequence, placed in MIS 3 between 50 and 40 ka BP, displays Mousterian artifacts, and represents a reference site to the study of the Middle to Upper Palaeolithic transition, and to Neanderthal behaviour in the last phases of their occupation of Central Italy.

Carrión et al. (2019) highlight the potential of Carihuela Cave for Neanderthal research in the southern Iberian Peninsula. Apart from providing new pollen records from carnivore coprolites, they analyse the available information regarding the chronology and palaeoecology of the Pleistocene deposits. From this they suggest working hypotheses for investigating not only the possibly late (i.e., MIS-3) persistence of some Neanderthal groups in the south of the Iberian Peninsula, but also, importantly, particular matters about MP chronology that remain unclear. A first step has to be that of systematic excavation at Carihuela by a multidisciplinary research team. Modern dating techniques, new analytical procedures, and novel proxies are required to test the tentative correlations proposed in the Carrión et al. (2019)'s paper. The importance of their study site is emphasised due to the abundance of finds including Palaeolithic artifacts and faunal material together with remains of both Neanderthal and anatomically-modern humans. This would complement the excellent preservation of coprolites, charcoal, pollen grains, spores and other microfossils suitable for palaeopalynological, botanical microscopy and anthracology.

In the paper "Following the last Neanderthals", Muñiz et al. (2019) study the mammalian footprints recognized in vertical cross sections and convex hyporeliefs from Catalan Bay, Rock of Gibraltar. Plausibly, these footprints belong to Homininae, Proboscidea, Artiodactyla and Carnivora. The affinity between the footprints and their tracemakers is supported by physical parameters, footprint morphology and correlation with the fossil fauna of

vertebrates described for the Late Pleistocene of Gibraltar. The finds involve the first palaeoichnological record in the aeolian sediments of Gibraltar and indirectly corroborate the occupation of the coastal dune landscape by several terrestrial mammals during the Late Pleistocene. The age of the tracks has been established as within MIS 3, during the probable Middle-Upper Palaeolithic transition in the climate refuge of Gibraltar.

According to conventional wisdom, diet broadening should be expected as a feature of Anatomically Modern Humans with fully sapient cognition. However, the Neanderthal use of small size prey is supported by a growing body of evidence, especially in the Mediterranean Basin. Nabais and Zilhao (2019) demonstrate the human collection and consumption of tortoises, together with a diversity of food resources, in two key Middle Palaeolithic cave sites of Portugal, Gruta de Oliveira and Gruta da Figueira Brava, dated at the Last Interglacial. Based on an improved osteometric method, in which long bone measurements are standardised and analysed together using the Logarithmic Size Index (LSI), it is possible to better gauge the contribution of tortoises to the diet and the human impact on the species' populations. At inland Gruta da Oliveira, a tendency towards the massive collection of tortoises, affecting the local population more severely, is visible. At coastal Gruta da Figueira Brava, the data suggest opportunistic collection upon encounter, possibly due to the availability of a more diverse range of resources. Nabais and Zilhao (2019) also discuss the nutritional benefits of small prey as an overall hunting strategy of Neanderthals.

Still in the field of hominin food behaviour, Cortés-Sánchez et al. (2019) find Middle and Early Upper Paleolithic evidence of shellfish collection on the southern Iberian site of Bajondillo cave. Clearly, Neanderthals were harvesting molluscs well before the arrival of anatomically modern humans in the region. Comparative analyses demonstrate that these Neanderthals were not exceptional by any means since the evidence of shellfishing during Mousterian times are also documented at other Alborán Sea sites. It is interesting here that the mollusc assemblages depict decreasing abundance from the earliest to the latest archaeological levels, in particular when *H. sapiens* replaced *H. neanderthalensis*. There is also an increased abundance of infaunal bivalves during the *H. sapiens* phase. Bajondillo cave shellfishing signals seem sensitive to the distance of the site to the coast and paleoenvironmental conditions. This may explain why the site provides evidences of shellfishing during MIS4, a poorly documented stage in terms of aquatic adaptations that is associated to a major sea level drop. A comparison between Bajondillo cave and Pinnacle Point show that infaunal bivalve abundances in the South African site are far higher than those recorded in the Middle Palaeolithic levels of Bajondillo.

Finlayson et al. (2019) yield clues to decipher a long human/Golden Eagle association going as far back as the Neanderthals, which doubtless, were able to catch birds (Finlayson et al., 2012). These authors contend that there is a group of bird species that appears to have been particularly targeted by Neanderthals, namely the largest diurnal raptors that were available to them, along with a group of medium-sized corvids and doves. The Golden Eagle was one of the targeted species, and it would seem both for feathers and talons were sought after. It is also shown here that the practice of targeting large raptors and corvids continued after the disappearance of the Neanderthals and the arrival of Moderns up to historical times.

Deeper in the palaeoecological terrain of Neanderthals, Carrión-Marco et al. (2019) have carried out charcoal and microfaunal analysis in the Abrigo de la Quebrada early Upper Pleistocene site, and discussed subsistence practices and local resource exploitation. Mountain pine forests and permanent grass formations containing

humid zones and open spaces that would have harboured a eurythermal microfauna were the dominant landscape type. The data are consistent with a recurrent, seasonal occupation pattern in which the rock shelter was used for short periods in the context of an annual round characterized by a high degree of mobility. Carrión-Marco et al. (2019) also provides taphonomic information, in particular on preservation issues. They find differences between levels which are determined by the dynamics of the sedimentary accumulation and of the human occupation of the site, i.e., a lower sedimentation rate and a higher intensity of the activities recorded in the upper levels versus a higher sedimentation rate and more sporadic nature of the human presence recorded in the basal levels. These authors add to the discussion on the controlled use of fire by Neanderthals.

Fire is one of the most debated issues in Palaeolithic archaeology. Rosell and Blasco (2019)'s paper is a thorough treatment on the beginnings of the regular use of fire between MIS 11 and MIS 9, a time of complex cultural and technological changes in Europe and the Near East including the emergence of the post-Acheulian lithic assemblages and all the associated shifts in social organisation and perceptions of inhabited spaces. The analysis suggests some general trends, but more interestingly leave several questions open for debate. Rosell and Blasco (2019) depict three principal lines of research to deal with these matters: to investigate how cultural acquisitions were implemented on a temporary basis, to explore why groups with and without fire technology coexisted during the first phase of assimilation and control, and finally to provide guidelines that might help better understand the processes of incorporating technological innovations into human ways of life throughout history.

Ochando et al. (2019) bring novel palaeoenvironmental data for the Middle and early Upper Pleistocene, MIS 9 to MIS 5, in a renowned cave site of early Neanderthals, Bolomor in Eastern Spain. The sequence is very rich in palynomorphs and highlights the long resilience of mixed oak-pine forests throughout cold phases and the high diversity of woody taxa including deciduous, Mediterranean, and thermophytes. The relative abundance of evergreen *Quercus* and *Castanea*, the continuous occurrences of *Olea*, *Fraxinus*, *Pistacia*, *Myrtus*, *Phillyrea* and *Cistaceae*, and the presence of *Celtis*, *Ceratonia*, *Pinus pinaster*, and *Rhododendron* are also worth mentioning. One of the most striking features of this new sequence is the occurrence of a dense forest landscape during glacial stages. The picture is supported by the mammalian faunal record. Ochando et al. (2019) also discuss the subsistence strategies of the Bolomor hominids, which took place in a diverse and rich environment where a broad spectrum of edible plants was available such as hazelnut (*Corylus avellana*), chestnut (*Castanea sativa*), Mediterranean hackberry (*Celtis australis*), strawberry tree (*Arbutus unedo*), carob tree (*Ceratonia siliqua*), holly oak (*Quercus ilex*), olive (*Olea europaea*), elderberry (*Sambucus nigra*), and probably wild Rosaceae such as several species of *Prunus*, *Rubus*, *Rosa*, and *Sorbus*. The study is also outstanding because there are very few paleobotanical studies of Neanderthals sites of the Eurasian Middle Pleistocene. The refugium hypothesis for Neanderthal long survival in the Iberian Peninsula (e.g. Carrión et al., 2018) is herein supported.

Greenbaum et al. (2019)'s work deals with the transitional techno-complexes occurring between the Middle Paleolithic (MP) and the Upper Paleolithic (UP). These authors try to explain the synchronous appearances of those techno-complexes using a common underlying driver, which would have been an increase in inter-population connectivity, both within- and between-species, thus allowing local cultures to rapidly evolve and to attain great complexity. The postulation is that this change was driven by the

interaction between modern humans and Neanderthals. The main focus is on the potential processes that would have influenced that inter-population connectivity, bringing together evolutionary and ecological perspectives alongside insights from the field of cultural evolution. A number of factors appear involved: inter-group and inter-species disease dynamics, introgression and the spread of adaptive introgressed genes, extinction-recolonization dynamics, and selection of genetically and/or culturally determined invasiveness-related traits. This approach is one of greater complexity respecting former interpretations such as those suggesting that the emergence of the transitional industries is related to the spread of Moderns in Eurasia (Hublin, 2015; Stutz, 2015) and that their driver is ‘acculturation’ of local groups by the arriving Moderns (Mellars, 2004), or that the cultural changes are an adaptive response to increased competition with the newcomers (Maíllo-Fernández, 2013; Shea, 2003).

Through a solid epistemological stance, Slimak (2018) addresses the extinction of Neanderthals from cultural anthropology, arguing that the extinction cannot be simplistically imputed to a conjunction of several natural processes. The author proposes that most theories about extinction cannot satisfy the evidence of adaptive ubiquity of the Neanderthal societies or the high diversity of territories in which they settled. Environmental changes including the disappearance of hunted fauna should be therefore considered as secondary in relation to the extinction of Neanderthals. Slimak suggests that we should conduct more research on the ethological and anthropological structures of Neanderthal populations, and provide methodological proposals to address the main issues arising in this respect. This would include the identification of an ethology of biologically fossil societies, which “cannot be evaluated based on the notions of presence/absence of archaeological realities to which we subjectively confer a discriminating function (a bone tool, an ornament, a grave, ...), but by exploring the logical identification of all the technical and cultural products of these societies”.

Doubtless, the extinction of Neanderthals and its connection with the arrivals of Modern Humans to Western Europe is still unclear, and the old debate continues about whether climate changes (Jiménez-Espejo et al., 2007; Stewart, 2005, 2004), ozone depletion associated to Laschamp-Mono lake geomagnetic event, and a consequent increase of the UV-B radiations (Valet and Valladas, 2010), assimilation into the genetic pool (Zilhão et al., 2010) or competition with Modern Humans (Gilpin et al., 2016) played the main role in driving Neanderthals to depletion and extinction. Kolodny and Feldman (2017) provide an alternative, in fact a neutral model of evolution in which Neanderthal replacement was determined by repeated migration of modern humans from Africa into Eurasia, followed by random species drift.

We can now trace back the demographic process of extinction from genetic data. Our genome is in fact a reflection of our past evolutionary history. Smaller populations have less genetic diversity and tend to accumulate deleterious mutations that can further compromise the future of the species. Endogamy and consanguinity result in genomic tracks that are identical in both chromosomal copies. These signs of a long-term demographic decline can be distinguished in high coverage Neanderthal and Denisovan genomes (Prüfer et al., 2014; Castellano et al., 2014) and may have exacerbated other disrupting factors like the ones mentioned above. Interestingly, similar genetic patterns are currently seen in species, such as the Iberian lynx, that are at risk of extinction, which suggests that Neanderthal's dynamics were not different from other extinction processes, both past and present. A complete understanding of the Neanderthal's fate would likely require additional genetic data as well as the integration of social,

biological and cultural evidences.

It cannot be stressed enough that the biological realities at this time are spatially complex and the geneticists have arrived to help us understand that there was much more gene flow than was assumed among all hominin populations investigated (Lalueza-Fox, 2017). Certainly, Neanderthals are extinct, but a number of their genetic variants persist today in modern humans of non-African descent. These derive on average 1–3% of their genome from Neanderthal ancestors that interbred with our own ancestors (Simonti et al., 2016). In addition, Denisovans were present (Krause et al., 2010; Stringer and Barnes, 2015), and it is also true that Neanderthals, Denisovans and other species hybridized in different regions and periods (Varki, 2016; Slon et al., 2018), and yet, they continued being genetically different to the point that we can perfectly recognize a Neanderthal-Denisovan hybrid (Slon et al., 2018). There are also “ghost species”, species for which we do not have bone records. In sum, by 40,000 years ago at least three different human species were present and competed with each other. This makes the conventional story of a simple and quick replacement less and less plausible and the whole story of evolutionary relationships more and more puzzling.

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References

- Bermúdez de Castro, J.M., Martín-Torres, M., Martínez de Pinillos, M., García-Campos, C., Modesto-Mata, M., Martín-Francés, L., Arsuaga, J.L., 2019. Metric and morphological comparison between the Arago (France) and Atapuerca-Sima de los Huesos (Spain) dental samples, and the origin of Neanderthals. *Quat. Sci. Rev.* 217, 45–61.
- Carrión-Marco, Y., Guillem Calatayud, P., Eixea, A., Martínez-Varea, C.M., Tormo, C., Badal, E., Zilhão, J., Villaverde, V., 2019. Climate, environment and human behaviour in the Middle Palaeolithic of Abrigo de la Quebrada (Valencia, Spain): the evidence from charred plant and micromammal remains. *Quat. Sci. Rev.* 217, 152–168.
- Carrión, J.S., Fernández, S., Jiménez, J., Munuera Giner, M., Ochando, J., Amorós, G., Ponce de León, M., Zollikofer, Ch., Martín-Lerma, I., Toro-Moyano, I., Hajdas, I., Walker, M.J., 2019. The sequence at Carihuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. *Quat. Sci. Rev.* 217, 194–216.
- Carrión, J.S., Ochando, J., Fernández, S., Munuera, M., Amorós, G., Blasco, R., Rosell, J., Finlayson, S., Giles, F., Jennings, R., Finlayson, G., Giles-Pacheco, F., Rodríguez-Vidal, J., Finlayson, C., 2018. Last Neanderthals in the warmest refugium of Europe: palynological data from Vanguard cave. *Rev. Palaeobot. Palynol.* 259, 63–80.
- Carrión, J.S., Walker, M.J., 2019. Background to neanderthal presence in Western Mediterranean Europe. *Quat. Sci. Rev.* 217, 7–44.
- Castellano, S., Parra, G., Sánchez-Quinto, F., Racimo, F., Kuhlwillm, M., Kircher, M., Sawyer, S., Fu, Q., Heinze, A., Nickel, B., Dabney, J., Siebauer, M., White, L., Burbano, H.A., Renaud, G., Stenzel, U., Lalueza-Fox, C., de la Rasiella, M., Rosas, A., Rudan, P., Brajkovic, D., Kucan, Z., Gušić, I., Shunkov, M.V., Derevianko, A.P., Viola, B., Meyer, M., Kelso, J., Andrés, A.M., Pääbo, S., 2014. Patterns of coding variation in the complete exomes of three Neanderthals. *Proc. Natl. Acad. Sci. USA* 111 (18), 6666–6671.
- Cortés-Sánchez, M., Simón-Vallejo, M.D., Jiménez-Espejo, F.J., Lozano Francisco, M.C., Vera-Peláez, J.L., Maestro González, A., Morales-Muñiz, A., 2019. Shellfish collection on the westernmost Mediterranean, Bajondillo cave (~160–35 cal kyr BP): a case of behavioral convergence? *Quat. Sci. Rev.* 217, 284–296.
- Di Vincenzo, F., Churchill, S.E., Buzi, C., Profico, A., Tafuri, M.A., Micheli, M., Caramelli, D., Manzi, G., 2019. Distinct among Neanderthals: the scapula of the skeleton from Altamura, Italy. *Quat. Sci. Rev.* 217, 76–88.
- Fernández-Jalvo, Y., Andrews, P., 2019. SPY CAVE (Belgium) Neanderthals (36,000y BP). Taphonomy and perimortem traumas of Spy I and Spy II: murder or

- accident. *Q. Sci. Rev.* 217, 119–129.
- Finlayson, C., Carrión, J.S., 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. *Trends Ecol. Evol.* 22, 213–222.
- Finlayson, S., Finlayson, G., Giles-Guzman, F., Finlayson, C., 2019. Neanderthals and the cult of the sun bird. *Quat. Sci. Rev.* 217, 217–224.
- Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J.J., Bortolotti, G.R., Finlayson, G., Sánchez-Marco, A., Giles Pacheco, F., Rodríguez-Vidal, J., Carrión, J.S., Fa, D.A., Rodríguez-Llanes, J.M., 2012. Birds of a feather: Neanderthal exploitation of raptors and corvids. *PLoS One* 7 (9), e45927.
- Gilpin, W., Feldman, M.W., Aoki, K., 2016. An ecocultural model predicts Neanderthal extinction through competition with modern humans. *Proc. Natl. Acad. Sci. USA* 113, 2134–2139.
- Greenbaum, G., Friesem, D.E., Hovers, E., Feldman, M.W., Kolodny, O., 2019. Was inter-population connectivity of Neanderthals and modern humans the driver of the Upper Paleolithic transition rather than its product? *Quat. Sci. Rev.* 217, 316–329.
- Gunz, P., Bulugina, E., 2012. The Mousterian child from Teshik-Tash is a Neanderthal: a geometric morphometric study of the frontal bone. *Am. J. Phys. Anthropol.* 149, 365–379.
- Gunz, Ph., Tilot, A.K., Wittfeld, K., Chin, A.T., Shapland, Y., van Erp, Th.G.M., Dannemann, M., Vernot, B., Neubauer, S., Guadalupe, T., Fernández, G., Brunner, H.G., Enard, E., Fallon, J., Hosten, N., Wölker, U., Profico, A., Di Vincenzo, F., Fisher, S.E., 2019. Neandertal introgression sheds light on modern human endocranial globularity. *Curr. Biol.* 29, 120–127.
- Hublin, J.-J., 2015. The modern human colonization of western Eurasia: when and where? *Quat. Sci. Rev.* 118, 194–210.
- Jiménez, J., Bienvenu, Th., Toro-Moyano, I., Ponce de León, M., Zollikofer, Ch., 2019. Virtual reconstruction and re-evaluation of the Neanderthal frontal bone from Carigüela Cave (Granada, Spain). *Quat. Sci. Rev.* 217, 89–97.
- Jiménez-Espejo, F., Martínez-Ruiz, F., Finlayson, C., Paytan, A., Sakamoto, T., Ortega, M., Finlayson, G., Iijima, K., Gallego, D., Fa, D., 2007. Climate forcing and Neanderthal extinction in southern Iberia: insights from a multiproxy marine record. *Quat. Sci. Rev.* 26, 836–852.
- Kolodny, O., Feldman, M.W., 2017. A parsimonious neutral model suggests Neanderthal replacement was determined by migration and random species drift. *Nat. Commun.* 8, 1040. <https://doi.org/10.1038/s41467-017-01043-z>.
- Krause, J., Fu, Q., Good, J.M., Viola, B., Shunkov, M.V., Derevianko, A.P., Pääbo, S., 2010. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. *Nature* 464, 894–897.
- Lalueza-Fox, C., 2017. A brief history of palaeogenomics: how a young discipline revolutionised the study of the past. *Métode Sci. Stud. J. Ann. Rev.* 8, 91–97.
- Maillo-Fernández, J.-M., 2013. Thoughts for discussion with regards to the middle-upper paleolithic transition in the Iberian Peninsula. In: Pastoors, A., Auffermann, B. (Eds.), *Pleistocene Foragers in the Iberian Peninsula. Their culture and environment*, pp. 107–122.
- Mellars, P., 2004. Neanderthals and the modern human colonization of Europe. *Nature* 432, 461–465.
- Moroni, A., Boschian, G., Crezzini, J., Montanari-Canini, G., Marciani, G., Capocchi, G., Arrighi, S., Aureli, D., Berto, C., Freguglia, M., Araujo, A., Scaramucci, S., Hublin, J.J., Lauer, T., Benazzi, S., Parenti, F., Bonato, M., Ricci, S., Talamo, S., Segre, A.G., Boschian, F., Spagnolo, V., 2019. Late Neandertals in central Italy. High-resolution chronicles from Grotta dei Santi (Monte Argentario - Tuscany). *Quat. Sci. Rev.* 217, 130–151.
- Muñoz, F., Cáceres, L.M., Rodríguez-Vidal, J., Neto de Carvalho, C., Belo, J., Finlayson, C., Finlayson, G., Finlayson, S., Izquierdo, T., Abad, M., Jiménez-Espejo, F., Sugisaki, S., Gómez, P., Ruiz, F., 2019. Following the last Neanderthals: mammal tracks in late Pleistocene coastal dunes of Gibraltar (S Iberian Peninsula). *Quat. Sci. Rev.* 217, 297–309.
- Nabais, M., Zilhão, J., 2019. The consumption of tortoise among last interglacial Iberian Neanderthals. *Quat. Sci. Rev.* 217, 225–246.
- Ochando, J., Carrión, J.S., Blasco, R., Fernández, S., Amorós, G., Munuera, M., Sanudo, P., Fernández Peris, J., 2019. Silvicolous Neanderthals in the far west: the mid-Pleistocene palaeoecological sequence of Bolomor cave (Valencia, Spain). *Quat. Sci. Rev.* 217, 247–267.
- Ponce de León, M.S., Bienvenu, T., Akazawa, T., Zollikofer, C.P., 2016. Brain development is similar in Neanderthals and modern humans. *Curr. Biol.* 226, 665–666.
- Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P.H., de Filippo, C., Li, H., Mallick, S., Dannemann, M., Fu, Q., Kircher, M., Kuhlwilm, M., Lachmann, M., Meyer, M., Ongyerth, M., Siebauer, M., Theunert, C., Tandon, A., Moorjani, P., Pickrell, J., Mullikin, J.C., Vohr, S.H., Green, R.E., Hellmann, I., Johnson, P.L.F., Blanche, H., Cann, H., Kitzman, J.O., Shendure, J., Eichler, E.E., Lein, E.S., Bakken, T.E., Golovanova, L.V., Doronichev, V.B., Shunkov, M.V., Derevianko, A.P., Viola, B., Slatkin, M., Reich, D., Kelso, J., Pääbo, S., 2014. The complete genome sequence of a Neandertal from the Altai Mountains. *Nature* 505, 43–49.
- Rosas, A., Bastir, M., Alarcón, J.A., 2019. Tempo and mode in the Neandertal evolutionary lineage: a structuralist approach to mandible variation. *Quat. Sci. Rev.* 217, 62–75.
- Rosell, J., Blasco, R., 2019. The early use of fire among Neanderthals from a zooarchaeological perspective. *Quat. Sci. Rev.* 217, 268–283.
- Scott, G.R., Turner, C.G., 1997. *The Anthropology of Modern Human Teeth. Dental Morphology and its Variation in Recent Human Populations*. Cambridge University Press, Cambridge, New York.
- Shea, J.J., 2003. Neandertals, competition, and the origin of modern human behavior in the Levant. *Evolut. Anthropol. Issues* 12, 173–187.
- Simonti, C.N., Vernot, B., Bastarache, L., Bottinger, E., Carrell, D., Chisholm, R.L., Crosslin, D.R., Hebringer, S.J., Jarvik, G.P., Kullo, I.J., Li, R., Pathak, J., Ritchie, M.D., Roden, D.M., Verma, S.S., Tromp, G., Prato, J.D., Bush, W.S., Akey, J.M., Denny, J.C., Capra, J.A., 2016. The phenotypic legacy of admixture between modern humans and Neandertals. *Science* 351, 737–741.
- Slimak, L., 2019. For a cultural anthropology of the last Neandertals. *Quat. Sci. Rev.* 217, 330–339.
- Slon, V., Mafessoni, F., Vernot, B., de Filippo, C., Grote, S., Viola, B., Hajdinjak, M., Peyrégne, S., Nagel, S., Brown, S., Douka, K., Higham, T., Kozlikin, M.B., Shunkov, M.V., Derevianko, A.P., Kelso, J., Meyer, M., Prüfer, K., Pääbo, S., 2018. The genome of the offspring of a Neandertal mother and a Denisovan father. *Nature* 561, 113–116.
- Spagnolo, V., Marciani, G., Aureli, D., Berna, F., Toniello, G., Astudillo, F., Boschian, F., Boscato, P., Ronchitelli, A., 2019. Neandertal activity and resting areas from stratigraphic unit 13 at the Middle Palaeolithic site of Oscuruscio (ginosa - Taranto, southern Italy). *Quat. Sci. Rev.* 217, 169–193.
- Spikins, P., Needham, A., Wright, B., Dytham, C., Gatta, M., Hitchens, G., 2019. Living to fight another day: the ecological and evolutionary significance of Neandertal healthcare. *Quat. Sci. Rev.* 217, 98–118.
- Stewart, J.R., 2004. Neandertal-modern human competition?: a comparison between the mammals associated with Middle and upper palaeolithic industries in Europe during OIS 3. *Int. J. Osteoarchaeol.* 14, 178–189.
- Stewart, J.R., 2005. The ecology and adaptation of Neandertals during the non-analogous environment of oxygen isotope stage 3. *Quat. Int.* 137, 35–46.
- Stewart, J.R., García-Rodríguez, O., Knul, M.V., Sewell, L., Montgomery, H., Thomas, M.G., Diekmann, Y., 2019. Palaeoecological and genetic evidence for Neandertal power locomotion as an adaptation to a woodland environment. *Quat. Sci. Rev.* 217, 310–315.
- Stringer, C.B., Barnes, I., 2015. Deciphering the Denisovans. *Proc. Natl. Acad. Sci. USA* 112, 15542–15543.
- Stutz, A.J., 2015. *The Protoaurignacian Didn't Trigger Anything* [WWW Document]. *Biocultural Evol. Blog Our Intertwined Biol. Cult. Identity*. <https://bioculturevolution.net/2015/06/12/the-Protoaurignacian-didnt-triggeranything/>.
- Valet, J.-P., Valladas, H., 2010. The Laschamp-Mono lake geomagnetic events and the extinction of Neanderthals: a causal link or a coincidence. *Quat. Sci. Rev.* 19, 3887–3893.
- Varki, A., 2016. Why are there no persisting hybrids of humans with Denisovans, Neanderthals, or anyone else? *Proc. Natl. Acad. Sci. USA* 113, 2354.
- Zilhão, J., Davis, S., Duarte, C., Soares, A.M., Steier, P., Wild, E., 2010. Pego do Diabo (Loures, Portugal): dating the emergence of anatomical modernity in westernmost Eurasia. *PLoS One* 5, e8880.