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## From linear measurements in multivariate analysis to computational palaeontology

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*KEY WORDS* - Phylogenetic comparative methods, geometric morphometrics, computational palaeontology, conservation palaeobiology, Artificial Intelligence, diversification rates.

*ABSTRACT* - Palaeontology, traditionally rooted in fieldwork and direct observation of fossil remains, is undergoing a transformative shift thanks to technological and mathematical innovations. These advances have expanded the scope and depth of palaeontological research, improving our understanding of evolutionary processes, shape evolution, phylogenetic relationships, and taxonomic diversification. Statistical tools, particularly phylogenetic comparative methods, have become essential for evaluating evolutionary rates and patterns across species. Geometric morphometrics has revolutionised the study of biological form, enabling more accurate reconstructions of fossilised organisms and detailed analyses of evolutionary trends. Additionally, new imaging technologies, such as scanning electron microscopy (SEM) and synchrotron radiation, have enhanced the study of fossils and opened new avenues for detailed analysis. In the last few years, Artificial Intelligence (AI) and machine learning, though still in their early stages, are showing promise for automating fossil classification, identifying patterns in large datasets, and even advancing image-based systematic taxonomy. While AI tools are not yet a replacement for expert palaeontologists, they offer significant support, particularly in curating large collections and facilitating rapid classification processes. However, the integration of all these statistical and technological tools into palaeontological practice presents challenges, particularly in terms of interpreting results accurately. This underscores the need for palaeontologists to develop a foundational understanding of the algorithms and statistical methods they employ, ensuring proper application and reducing the risk of erroneous inferences. As these mathematical and computational tools continue to evolve, they are set to revolutionise palaeontology, enabling more efficient, accurate, and innovative research. Furthermore, these advancements are contributing to the growing field of conservation palaeobiology, with potential applications in understanding climate change, extinction events, and species adaptation, offering critical insights into contemporary conservation efforts.

### INTRODUCTION

A middle-aged man lies on the floor, belly down. He is all alone, in the middle of nowhere, soaked with perspiration under a scorching sun. Holding a brush and dusty dentist tools, he is focusing on tiny, glassy-brown, scattered bone splinters half emerged from the rock surface. Despite the discomforting settings, his face is not the one you would expect for an exhausted man of his age, overwhelmed by the unforgiving warmth and hours of labor. Quite the opposite, his glaring facial expression delivers the idea that he is on something exceptional that he can anticipate in his mind, some great news that he will share to pals, in science and beyond, in the months to come. That face is wearing, you can imagine, the pleasure that comes with great discoveries, that momentous instant when long and strenuous days of fieldwork finally reroute towards glory. This kind of romantic, old-fashioned image

is what most laypeople would fathom at thinking about our profession, one where you perform in boots and boonie hat, making for barren heaths in search of quirk evidence of life left behind millions of years ago. Change boots with 20<sup>th</sup> Century middle-class suits (or hats with poke bonnets, if you wish), add hordes of underpaid workers lined in bringing hefty wood boxes full of carved rocks, and you get a more mundane perhaps, but certainly still veritable impression of what this profession used to be in its early days, by the deeds of heroic people such as Raymond Dart, Dorothea Bate and Mary Anning. People like them and others such as Thomas Huxley, Edward Cope, and Othniel Marsh were probably the epitome figures of such palaeontological *ancien régime*. The latter two even fought the bloody "bone wars" (Kurtz, 2023) that first let our discipline gracing newspaper headlines and brought American palaeontology at the frontline of dinosaur research. It was Huxley's family, though, to fame

the mathematical approach in the field of evolutionary studies. Best known for his lively defence of Charles Darwin's theory (without which we would perhaps still be talking about petrified tongues or misused organs), Thomas Huxley has, among his many other achievements and the vast influence on the diffusion of the scientific thought in education, installed the sense of scientific method in his own children and grandchildren's upbringing. The fertile Huxley's manor let his grandson Julian to produce the power law describing allometry (Gayon, 2000) and Julian's half-brother Andrew to become a Nobel laureate in Physiology. The Huxleys foreshadowed a great transition in the field of palaeontology, from digging out and describing fossils and the history of life, ascertaining the age of fossil horizons and highlighting and understanding the impact of climate change to mostly the same digging, describing and evaluating the impact of climate as of today. We mean that whereas palaeontology has obviously remained the same, cherishes the same material and pursues almost the same goals as ever, the great transition rests in the methods, the upended how to makes it. This enduring changeover has never been a continuous process (neither it is expected to be since science does not proceed this way; Kuhn, 1997) (Fig. 1). Instead, it was marked by intermittent leaps forward, each bringing new methods and technological advancements in the everyday life of palaeontology practitioners, with immeasurable and often unanticipated consequences. Take the science of classification as an example. Although most palaeontological classification is still filled with phenetics, today palaeontologists name biological remains and produce species (phylogenetic) trees trying to elucidate the polarity of character states, to isolate apomorphic traits, and to apply some form of parsimony principle, striving not just to produce what they think is the "correct" phylogenetic tree or best naming arrangement, but more aptly to generate feasible trees and classification schemes which legitimately represent the history of life. The very moment when the old motto that "it is true that a common origin implies some similarity while the converse is not necessarily true" moved from being verbal to factual, was when the German entomologist Willi Henning invented cladistics (Dupuis, 1984) (Fig. 1). Same thing later again, when Svante Pääbo managed to recollect ancient DNA from fossil remains, paving the ground for ancient DNA studies (Pääbo, 1985; Cann et al., 1987). As with cladistics (Gee, 2001), the study of palaeogenetics is revolutionising the field, and producing new tools and findings which are changing the way we practice our beloved discipline, the way we understand our precious fossils, and the very concept of species and their existence (Orlando & Cooper, 2014; Cahill et al., 2018; Slon et al., 2018; Cappellini et al., 2019; Ruan et al., 2023). There are many other examples of the great transition in the making, which we will comment upon on the next section, to highlight that the transition has two components, that are intermingled and yet maintain a clearly separate genesis. One is technological, the other is methodological. In the closing lines of this introduction section, we wish instead to emphasise that the great transition, which, for the sake of simplicity we could describe as a long, stepwise move from pure description to mathematical analysis of the discipline content, is not new to palaeontology, neither to

science. In ecology, the transition was guided by Robert MacArthur, who championed the idea that ecological theory should be grounded in mathematical modelling and proof (Brown, 1999) and was first advocated in evolutionary studies by the great American palaeontologist George Gaylord Simpson and his wife Anne Roe in their 1960 book *Quantitative Zoology* (Simpson et al., 2003). Everything that came later is part of a more general shift towards quantitative science, which in the case of palaeontology is, we defend, finally reinstalling the discipline where it rightfully belongs, sat at the high table of evolution (Gould, 1994).

#### *Armchair palaeontology, methodological advances to the non-physical study of past life*

To those who love digging out fossils, the primary accusation to others indulging in mathematical and statistical modelling of the fossil record is to act as "armchair" palaeontologists. The definition of armchair scientist regards everybody contributing to a field without collecting primary data but providing synthesis and novel analysis by using the data published by others. The definition is deprecative, hinting at a "parasitic" behaviour of those sat on their chairs (or better in front of a computer monitor), at the expense of those brandishing shovels and pickaxes and doing all the hard work. Put in the words of the eminent American naturalist Edward Wilson: "The annals of theoretical biology are clogged with mathematical models that either can be safely ignored or, when tested, fail" (Wilson, 2013, p. 837). The bitter response to Wilson's bitter Wall Street Journal editorial was not long in coming. The Berkley mathematician Edward Frenkel retorted that "with the advent of the 3-D printing and other new technology, the reality we are used to is undergoing a radical transformation: everything will migrate from the layer of physical reality to the layer of information and data" (Frenkel, 2013, p. 838).

Nearly twelve years later we know who was right. Frenkel was also right into stating that with mathematics we learned Earth is not flat, not to mention Galileo's famous stance on mathematics as the language of the laws of Nature or Einstein's (the archetypal armchair physicist) opinion on the aesthetic appeal of mathematics. Wilson sourness against calculus was probably fuelled by his own *mathematical illiteracy* (Wilson's words in italics). This is not uncommon in the scientific tradition, and in the past has led to unusually bitter comments (up to accusations of producing witchcraft that nobody could understand) against published models and equations (most notably the Navier-Stokes equations which describe viscous fluids, that eventually provided the machinery to create something as innocent as computer graphics; Morris et al., 2023). Wilson noted that most great scientists were poor at maths and praised intuition and fieldwork instead, in addressing young scientists. It is hard to be against any of Wilson's statements, except for the main argument of his invective. Mathematics was important then, and it is becoming superbly important now. Without the handwritten work of people like Ronald Fisher, William Gosset (who signed his most important opera as "Student"), Adrien-Marie Legendre or Johann Gauss we would not have analysis of variance, t-test, and regression analysis, respectively, in our statistical

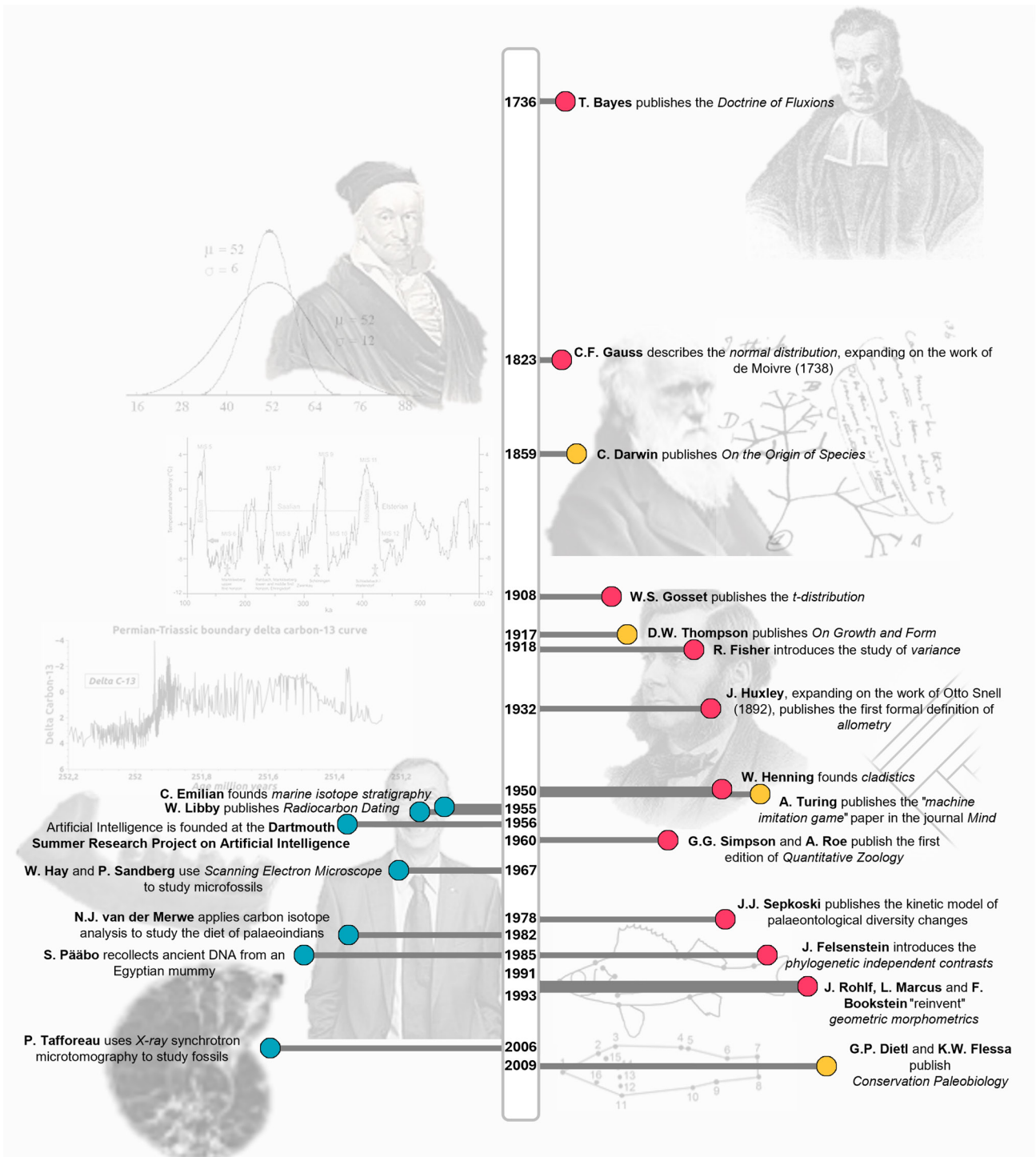


Fig. 1 - (color online) The timeline of major technological and statistical breakthroughs producing the transition and the main theories linked to these advancements. Major technological advancements are placed to the left. On the right, the most important statistical and theoretical improvements in the discipline.

toolbox (Fig. 1). And yet, since nobody fears such simple statistical tests, we feel nobody should fear machine learning or Bayesian methods (ironically, Thomas Bayes' *Doctrine of Fluxions* was published in 1736, the same year when accusing people of practicing witchcraft became a crime in Great Britain). Conversely, we are about to illustrate three examples of how mathematics came to dominate typical research areas in palaeontology, that is

the study of shape evolution, phylogenetic effects, and taxonomic diversification. These major "revolutions" took their top positions as the most commonly-applied methods in biology and palaeontology through a seamless, unscathed process that has not taken, we feel, anybody away from palaeontology, or scared anybody, but has instead expanded and diversified our discipline towards unanticipated stretches.

Traditional morphometrics was founded on bivariate plots. Immediately after the age of pure phenetics and the splendid hand drawings of early palaeontology, scientists began to advocate bivariate (Cartesian) plots as means of comparing the gross anatomy of remains, distinguishing species and reforming taxonomy, and most late 1900s palaeontologists followed in this tradition. For decades, bivariate plots have been the analytical tool of choice for separating species or tracing size trends over time. The problem is that bivariate plots are only visualisations, and the values on the x and y axes are only good at providing a very schematic representation of the biological objects they describe. Multivariate linear measurements, while inherently richer than bivariate data sets, are not necessarily better (Danilo Torre pioneered applying multivariate statistics in palaeontology in some of his early papers such as Micheli & Torre, 1965 and Torre, 1965). They usually fail capturing the inherent complexity of phenotypes and are plagued by collinearity and allometric effects (Adams et al., 2004). The only complete representation of a biological object is, of course, the shape of the object itself. The goal of describing shape in a more satisfactory way than just using simple and non-independent linear measurements has been considered mathematically intractable for nearly a century, despite D'Arcy Thompson's first publication of diffeomorphism (along with dozens of bivariate plots) in 2-D viewed fishes, copepods and other critters (Thompson, 1917) (Fig. 1). The Scottish biologist's dream only came to life nearly a century later, when Jim Rohlf (a biologist so proficient in maths to write along with his professor Robert Sokal a book of statistics cited more than 100,000 times), Leslie Marcus (a palaeontologist) and Fred Bookstein (a mathematician) reinvented Thompson's idea and founded the field of geometric morphometrics (Bookstein, 1991; Rohlf & Marcus, 1993). Hit "geometric morphometrics" in google scholar and you will get > 33,000 titles, restrict the research to year 1993 and you get 11. We can hardly imagine any clearer illustration of the success of the discipline. Over the years, geometric morphometrics (GM) has been enhanced by layers of complexity and refinements, becoming the prominent tool for studying ontogeny, adaptation, integration of biological parts into the phenotype and shape evolution (Mitteroecker et al., 2005; Adams et al., 2011; Sheets & Zelditch, 2013; Bookstein, 2015; Adams, 2016; Felice & Goswami, 2018; Adams & Collyer, 2019; Castiglione et al., 2019a; Piras et al., 2020; Goswami et al., 2022). Current GM methods are so refined that they can be applied to reconstruct the shape of shattered fossils (Zollikofer et al., 2005; Gunz et al., 2009; Cuff & Rayfield, 2015; Schlager et al., 2018; Profico et al., 2019), visualise evolutionary rates (Castiglione et al., 2022; Melchionna et al., 2024), and analyse biological objects that cannot be studied otherwise because of their rounded, dull shape, most notably the skull endocasts (Neubauer et al., 2009, 2018; Gunz et al., 2010; Neubauer & Hublin, 2012; Gunz & Mitteroecker, 2013; Bruner & Beaudet, 2023; de Sousa et al., 2023; Sansalone et al., 2023; Chiappe et al., 2024). Palaeontologists and palaeoanthropologists such as Goswami, Gunz, Mitteroecker, Neubauer, Polly, and Piras are not just using GM, they are innovating the field. An entirely new discipline, virtual palaeontology, has been founded, and is

adding new dimensions to the study of fossils by providing brand new analytical tools to the investigation of fossil remains (Weber, 2015; Lösel et al., 2020, 2023; Pandolfi et al., 2020; Profico et al., 2020, 2021).

There is one additional reason why bivariate and multivariate data are not well suited to study biological variation. Most statistical tests require that datapoints are independent from one another. In life sciences, shared ancestry means they are not. This simple observation revolutionised the comparative biology field (that is any application where measurements are compared across species) in the early 1980s, when Joseph (Joe) Felsenstein first introduced a mean to account for phylogenetic interrelationships (Felsenstein, 1985; Martins & Hansen, 1997) (we believe any palaeontologist should look at figure 7 in Felsenstein's 1985 paper before ditching phylogenetic effects as "unimportant"). Felsenstein idea was to use species trait values not as they are, but rather as they are "minus" what they should be after a phylogenetic expectation is accounted for, resulting in normally distributed phenotypic changes accumulating over time with unit variance and mean equal to zero. These deviations, or "contrasts" in the definition of Felsenstein, are truly independent of phylogeny, provided evolution proceeds at a constant rate and with net zero change, so that the "phylogenetic mean" corresponds to the phenotypic value at the tree root (this is the so-called Brownian motion model). Felsenstein's innovation was so shattering that we know of almost no paper published on decent venues presenting regressions between biological traits without accounting for phylogenetic effects. It is as if Felsenstein's phylogenetic comparative method (PCM) "killed" the good old bivariate plots and regressions, and most multivariate data analyses (Fig. 1). Of course, the Brownian motion is just a possible mode of evolution. More complicated, multi-rate models, even including a trend in the data (after all we palaeontologists are especially interested in deviations from the Brownian motion) were published since, and some are even especially meant to work with fossil, and to locate in time and across the tree instances of rate shifts and trends (Huelsenbeck & Ronquist, 2001; Rabosky, 2014; Castiglione et al., 2018, 2019b). R packages written to perform such analyses, like "phytools" (Revell, 2012), "Geiger" (Harmon et al., 2008) and "ape" (Paradis & Schliep, 2019) became extremely popular since (they were collectively downloaded >  $6 \cdot 10^6$  times as we write this manuscript). In modern palaeontology, at least when working at the interspecific level, the use of any PCM is almost mandatory. PCMs are bringing palaeontological research back at the forefront of evolutionary biology, providing the key evidence for the likelihood of evolutionary trends to apply (Hone & Benton, 2005; McNamara et al., 2006; Benton, 2009; Raia et al., 2012; Benson et al., 2014; Žliobaitė et al., 2017; Silvestro et al., 2020; Brocklehurst & Benson, 2021; Žliobaitė, 2024).

The last issue we will deal with is diversification. The analysis of species birth and death rates is at home in palaeontology. Early students of diversification rates introduced mathematical treatments of species counts across stratigraphic layers to derive speciation and extinction rates directly from the fossil record (Fig. 1). Championed by Jack Sepkoski, and later by Mike Foote,

John Alroy and Daniele Silvestro (Sepkoski et al., 1981; Alroy, 1994, 2008; Sepkoski, 1998; Foote, 2000; Silvestro et al., 2011, 2014) all these methods rely on the fossil record to infer the rates and all but one were developed by palaeontologists (Silvestro is a computational biologist). At some point, it became possible to infer diversification directly from phylogenetic trees, that put non-palaeontologists at ease with diversification analysis and allows adding the phylogenetic dimension (Sanderson & Donoghue, 1994; Adams et al., 2009; Raia et al., 2011; Stadler, 2011; Morlon, 2014; Didier et al., 2017; Maliet et al., 2019; Title & Rabosky, 2019). Unfortunately, extinction rates cannot be estimated by using phylogenetic trees (Rabosky, 2010) and trees of extant species may derive from multiple diversification histories (Louca & Pennell, 2020) and are biased towards inferring higher rates in the recent (O'Meara & Beaulieu, 2024). These limitations imply the primacy of the fossil record to study diversification is still probably there, and palaeontologists remain at the edge of diversification studies. With such a brilliant past and promising present, we feel the study of diversification rates is one where young palaeontologists should excel and should therefore strive to include as much statistics as possible in their curricula.

*The illiterate mathematician and how technological innovations produce better, more fruitful palaeontology*

In contrast to algorithms, the adaptation of technological innovations from other disciplines to study the fossil record is a less problematic approach and is likely to be less susceptible to misinterpretation and erroneous inferences. For those engaged in the study of fossils, one of the earliest of these innovations was Cesare Emiliani's isotopic palaeontology. Based on the work of Harold Urey, a Nobel laureate in Chemistry, the Italian micropalaeontologist devised the marine isotope stage (MIS) timescale, coined the term "palaeoceanography", and was the first to confirm Milankovitch's theory tenet that climatic variation is prompted by variations in Earth's orbit (Berger, 2002). Emiliani's pioneering work (Fig. 1) is rivalled in significance only by that of another remarkable innovator, Willard Libby, who, like Emiliani, was associated with Urey and, like Urey, was awarded the Nobel Prize in Chemistry (and was involved by Urey in the Manhattan Project). Libby is credited with developing the  $^{14}\text{C}$  dating method, which had a transformative impact on the fields of near-time palaeontology and palaeoanthropology. Although Libby was not himself a palaeontologist, it was palaeontologists and palaeoanthropologists who refined (and continue to refine today) absolute dating methods (Higham, 2011; Deviese et al., 2018; Grün & Stringer, 2023) showing that direct competence of the problem under scrutiny affords the unique opportunity to give any method an even better look than it originally had. Isotopic palaeontology was further expanded by the work of people like Nikolaas van der Merwe, who first used stable isotope analysis (the  $\delta^{13}\text{C}$  method) to study early hominin diets. Van der Merwe's results were later confirmed, finally reconciling inference drawn from classic morphological observation with isotope analysis (Henry et al., 2012; Sponheimer et al., 2013). To micropalaeontologists the great leap forward in terms of the depth of investigation came

with the introduction of Scanning Electron Microscope (SEM; Hay & Sandberg, 1967). SEM revolution changed micropalaeontology forever and a form of cyclic particle accelerator, the synchrotron, is promising to do the same to palaeontology as a whole (Tafforeau et al., 2006).

## DISCUSSION

Technology is at the heart of scientific progress. In recent years, artificial intelligence (AI) tools have helped boosting the technology push in science. These tools, and a branch of AI in particular, machine learning, are helping produce new research avenues and ideas (Xu et al., 2021). The trend is expected to increase (Fig. 1), as new tools are becoming available as ordinary software diffused through widely used platforms such as Matlab and R (Lang et al., 2019; Pichler & Hartig, 2023; Zhang et al., 2024). In the field of palaeontology, AI use is still at its infancy, although recent research efforts help the classification of carbonate facies (Dawson et al., 2023) and planktonic foraminifera (Marchant et al., 2020; Piva et al., 2024), and are even promising to produce image-based systematic taxonomy (Liu et al., 2023; Marret, 2023). AI papers often present 90% accuracy in classification as evidence of how good the AI tool is. Although we easily understand such high accuracy should be taken as solid indication that an algorithm works fine, from the perspective of a palaeontologist presenting new material or addressing its taxonomic status we suspect up to 10% of misclassification is far less exciting. This suggests automatic AI classifiers currently seem better suited to help museum or academic collection curators than professional palaeontologists. As they stand, AI tools providing automatic classification of cut marks in palaeoanthropology (Byeon et al., 2019) or taxonomic identification via bone peptides recognition in proteogenomics (Yang et al., 2021) seems much better oriented towards serving scientific research goals. Another fundamental aspect to consider is that AI needs previous knowledge to learn from, and previous knowledge means competent stratigraphers and taxonomists publishing their findings and providing illustrations of their work (Marret, 2023). Hence, since there is no point at running classifiers without robust palaeontological libraries, we wonder whether the best use of AI isn't just to save time and money, when large collections and restricted personnel are limiting factors. This does not mean "classical" palaeontologists should mind their business as usual and get rid of any AI, or worse any maths at all. Quite the opposite, we feel it is important to realise that although not all scientists could be, or are expected to be, fluent in mathematics, as the years pass it will become more and more important to understand how the algorithms work and are principled. This bare minimum will help keep track of new advancements and the fundamental message any of them delivers.

We focused upon the upsurge of AI just because it is the latest of a long series of technological and statistical innovations that were employed in palaeontology without even requiring scientists to fully understand what is going on with the algorithm they apply. However, this

attitude is, and always was, open to problems in the application and interpretation of the results, mostly depending on poor knowledge of the algorithms' assumptions, limits and functioning. This "black box" approach problem (Muhlbacher et al., 2014) stems from the general illiteracy in mathematics, which slows down the scientific progress (Chitnis & Smith, 2012) and even makes equations-containing papers less cited than more "verbal" articles (Fawcett & Higginson, 2012). Worse than anything else, the black box approach could produce wrong or biased inference by otherwise well-trained, expert palaeontologists. This is yet another reason palaeontologists, indeed any scientist, should train in maths at the best of their possibilities. After all, even Albert Einstein first published his *Entwurf* (outline) paper with a miscalculation (O'Raifeartaigh et al., 2017). What scientists from any field really need to avoid is being presented with research they cannot judge. In this case, either they need an expert co-author telling what is going on with the numbers, such as with Dobzhansky who got regularly instructed by Sewall Wright about the mathematics in their papers (we address the reader to the amusing footnotes in Gould, 1994, to know more about this). Alternatively, scientists risk falling victim to hoaxes, such as the infamous, nonsensical social science paper published by mathematician Alan Sokal in 1996 (Sokal, 2000). More commonly, however, the risk lies in losing touch with the cutting-edge research within their own field.

### CONCLUSIVE REMARKS

In his provocative *Is palaeontology a waste of public money?* article (Carnall, 2016) in "The Guardian", palaeontologist and science writer Mark Carnall notes with witty style: "Are extinction rates in rugose corals really as high impact to society as medical advances?" among other lines apparently slashing what he pretends palaeontology to be: just "the sexier side of geology". Carnall's rhetoric is, of course, in defense of palaeontology. He deliberately raises a straw lion and then kills it, just to explain why palaeontology matters (what else could Carnall's article be to a typical "Guardian reader" like the senior author of this manuscript?). In a synthesis, Carnall states that palaeontology matters because it is cheaper than most extravagant and regularly failing alternatives, and, as the most important reason, because, and we quote: "It can inform modern biological conservation". Carnall's thesis is at the heart of a new sub-discipline within our field called conservation palaeobiology. First theorised by Gregory Dietl and Karl Flessa (Dietl & Flessa, 2011) conservation palaeobiology promises to aid biological conservation by telling how species reacted to ravenous hunter-gatherers and changing climates during the (arguably) Late Pleistocene (Barnosky et al., 2017; Kiessling et al., 2019). Unfortunately, conservation palaeobiology has not lived up to its boasting promises (Dillon et al., 2022; Walker, 2023; Wingard et al., 2024) possibly due to a lack of focus on the relevant (for present-day ecosystems) temporal scale of observations as compared to the effects of climate change (Kiessling

et al., 2023). However, the sub-discipline is still alive and kicking and is finally starting to provide important information for conservationists in the near future (Saupe et al., 2015; Kiessling et al., 2019; Antell et al., 2021; Mondanaro et al., 2021, 2023; Belfiore et al., 2024; Malanoski et al., 2024). Conservation palaeobiology roots in the long tradition of palaeontological studies addressing climate change and climate crisis (De Lange et al., 2008; Erba et al., 2010; Bini et al., 2019) and climatic effects on extinction in general (Nogués-Bravo et al., 2018; Nolan et al., 2018; Saltré et al., 2019; Raia et al., 2020; Stewart et al., 2021; Bergman et al., 2023). With so much at stakes and so much to tell, it is likely we may anticipate a bright, although more math-oriented, future for palaeontology. New papers are coming out (Timmermann et al., 2024) specifically addressing how to use and develop algorithms, now that computer power, the resolution of climatic emulators, and large compilations of the fossil record (Faurby et al., 2018; Soria et al., 2021; Matthews et al., 2024) are all providing new opportunities and avenues for research which young palaeontologist could afford grasping.

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### REFERENCES

- Adams D.C. (2016). Evaluating modularity in morphometric data: Challenges with the RV coefficient and a new test measure. *Methods in Ecology and Evolution*, 7: 565-572.
- Adams D.C. & Collyer M.L. (2019). Phylogenetic Comparative Methods and the Evolution of Multivariate Phenotypes. *Annual Review of Ecology, Evolution, and Systematics*, 50: 405-425.
- Adams D.C., Rohlf F.J. & Slice D.E. (2004). Geometric morphometrics: Ten years of progress following the 'revolution.' *Italian Journal of Zoology*, 71: 5-16.
- Adams D.C., Berns C.M., Kozak K.H. & Wiens J.J. (2009). Are rates of species diversification correlated with rates of morphological evolution? *Proceedings of the Royal Society B: Biological Sciences*, 276: 2729-2738.
- Adams D.C., Cardini A., Monteiro L.R., O'Higgins P. & Rohlf F.J. (2011). Morphometrics and phylogenetics: Principal components of shape from cranial modules are neither appropriate nor effective cladistic characters. *Journal of Human Evolution*, 60: 240-243.
- Alroy J. (1994). Appearance event ordination: a new biochronologic method. *Paleobiology*, 20: 191-207.
- Alroy J. (2008). Dynamics of origination and extinction in the marine fossil record. *Proceedings of the National Academy of Sciences*, 105(supplement 1): 11536-11542.
- Antell G.S., Fenton I.S., Valdes P.J. & Saupe E.E. (2021). Thermal niches of planktonic foraminifera are static throughout glacial-interglacial climate change. *Proceedings of the National Academy of Sciences*, 118: 1-9.
- Barnosky A.D., Hadly E.A., Gonzalez P., Head J., Polly P.D., Lawing A.M., Eronen J.T., Ackerly D.D., Alex K., Biber E., Blois J., Brashares J., Ceballos G., Davis E., Dietl G.P., Dirzo R., Doremus H., Fortelius M., Greene H.W., Hellmann J., Hickler T., Jackson S., Kemp M., Koch P.L., Kremen C., Lindsey E.L., Looy C., Marshall C.R., Mendenhall C., Mulch A., Mychajliw

- A., Nowak C., Ramakrishnan U., Schnitzler J., Das Shrestha K., Solari K., Stegner L., Stegner M.A., Stenseth N.S., Wake M. & Zhang Z. (2017). Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*, 355(6325): eaah4787.
- Belfiore A.M., Mondanaro A., Castiglione S., Melchionna M., Girardi G., Raia P. & Di Febraro M. (2024). Too much of a good thing? Supplementing current species observations with fossil data to assess climate change vulnerability via ecological niche models. *Biological Conservation*, 291: 110495.
- Benson R.B.J., Frigot R.A., Goswami A., Andres B. & Butler R.J. (2014). Competition and constraint drove Cope's rule in the evolution of giant flying reptiles. *Nature Communications*, 5: 1-8.
- Benton M.J. (2009). The Red Queen and the Court Jester: Species diversity and the role of biotic and abiotic factors through time. *Science*, 323(5915): 728-732.
- Berger W.H. (2002). Cesare Emiliani (1922-1995), pioneer of Ice Age studies and oxygen isotope stratigraphy. *Comptes Rendus Palevol*, 1: 479-487.
- Bergman J., Pedersen R.Ø., Lundgren E.J., Lemoine R.T., Monsarrat S., Pearce E.A., Schierup M.H. & Svenning J.-C. (2023). Worldwide Late Pleistocene and Early Holocene population declines in extant megafauna are associated with *Homo sapiens* expansion rather than climate change. *Nature Communications*, 14: 7679.
- Bini M., Zanchetta G., Perşoiu A., Cartier R., Català A., Cacho I., Dean J.R., Di Rita F., Drysdale R.N., Finnè M., Isola I., Jalali B., Lirer F., Magri D., Masi A., Marks L., Mercuri A.M., Peyron O., Sadori L., Sicre M.-A., Welc F., Zielhofer C. & Brisset E. (2019). The 4.2kaBP Event in the Mediterranean region: an overview. *Climate of the Past*, 15: 555-577.
- Bookstein F.L. (1991). *Morphometric Tools for Landmark Data: Geometry and Biology*. 435 pp. Cambridge University Press, Cambridge.
- Bookstein F.L. (2015). Integration, Disintegration, and Self-Similarity: Characterizing the Scales of Shape Variation in Landmark Data. *Evolutionary Biology*, 42: 395-426.
- Brocklehurst N. & Benson R.J. (2021). Multiple paths to morphological diversification during the origin of amniotes. *Nature Ecology & Evolution*, 5: 1243-1249.
- Brown J.H. (1999). The Legacy of Robert MacArthur: from Geographical Ecology to Macroecology. *Journal of Mammalogy*, 80: 333-344.
- Bruner E. & Beaudet A. (2023). The brain of *Homo habilis*: Three decades of paleoneurology. *Journal of Human Evolution*, 174: 103281.
- Byeon W., Domínguez-Rodrigo M., Arampatzis G., Baquedano E., Yravedra J., Maté-González M.A. & Koumoutsakos P. (2019). Automated identification and deep classification of cut marks on bones and its paleoanthropological implications. *Journal of Computational Science*, 32: 36-43.
- Cahill J.A., Heintzman P.D., Harris K., Teasdale M.D., Kapp J., Soares A.E.R., Stirling I., Bradley D., Edwards C.J., Gream K., Kisleika A.A., Malev A.V., Monaghan N., Green R.E. & Shapiro B. (2018). Genomic Evidence of Widespread Admixture from Polar Bears into Brown Bears during the Last Ice Age. *Molecular Biology and Evolution*, 35: 1120-1129.
- Cann R.L., Stoneking M. & Wilson A.C. (1987). Mitochondrial DNA and human evolution. *Nature*, 325(6099): 31-36.
- Cappellini E., Welker F., Pandolfi L., Ramos-Madriral J., Samodova D., Rüter P.L., Fotakis A.K., Lyon D., Moreno-Mayar J.V., Bukhsianidze M., Rakownikow Jersie-Christensen R., Mackie M., Ginolhac A., Ferring R., Tappen M., Palkopoulou E., Dickinson M.R., Stafford T.W., Chan Y.L., Götherström A., Nathan S., Bruford M., Moodley Y., Agustí J., Kahlke R., Kiladze G., Martínez-Navarro B., Liu S., Sandoval Velasco M., Sinding M., Kelstrup C., Allentoft M., Krogh A., Orlando L., Penkman K., Shapiro B., Rook L., Dalen L., Gilbert M.T.P., Olsen J.V., Lordkipanidze D. & Willerslev E. (2019). Early Pleistocene enamel proteome sequences from Dmanisi resolve *Stephanorhinus* phylogeny. *Nature*, 574(7776): 103-107.
- Carnall M. (2016). *Is palaeontology a waste of public money?* The Guardian. <https://www.theguardian.com/science/2016/nov/09/is-palaeontology-a-waste-of-public-money>
- Castiglione S., Tesone G., Piccolo M., Melchionna M., Mondanaro A., Serio C., Di Febraro M. & Raia P. (2018). A new method for testing evolutionary rate variation and shifts in phenotypic evolution. *Methods in Ecology and Evolution*, 9: 974-983.
- Castiglione S., Serio C., Mondanaro A., Di Febraro M., Profico A., Girardi G. & Raia P. (2019a). Simultaneous detection of macroevolutionary patterns in phenotypic means and rate of change with and within phylogenetic trees including extinct species. *PLoS ONE*, 14: 1-13.
- Castiglione S., Serio C., Tamagnini D., Melchionna M., Mondanaro A., Di Febraro M., Profico A., Piras P., Barattolo F. & Raia P. (2019b). A new, fast method to search for morphological convergence with shape data. *PLoS ONE*, 14: e0226949.
- Castiglione S., Melchionna M., Profico A., Sansalone G., Modafferi M., Mondanaro A., Wroe S., Piras P. & Raia P. (2022). Human face-off: a new method for mapping evolutionary rates on three-dimensional digital models. *Palaeontology*, 65: 1-10.
- Chiappe L.M., Navalón G., Martinelli A.G., Carvalho I. de S., Miloni Santucci R., Wu Y.-H. & Field D.J. (2024). Cretaceous bird from Brazil informs the evolution of the avian skull and brain. *Nature*, 635(8038): 376-381.
- Chitnis N. & Smith T.A. (2012). Mathematical illiteracy impedes progress in biology. *Proceedings of the National Academy of Sciences*, 109: E3055-E3055.
- Cuff A.R. & Rayfield E.J. (2015). Retrodeformation and muscular reconstruction of ornithomimosaurian dinosaur crania. *PeerJ*, 2015: e1093.
- Dawson H.L., Dubrule O. & John C.M. (2023). Impact of dataset size and convolutional neural network architecture on transfer learning for carbonate rock classification. *Computers & Geosciences*, 171: 105284.
- De Lange G.J., Thomson J., Reitz A., Slomp C.P., Speranza Principato M., Erba E. & Corselli C. (2008). Synchronous basin-wide formation and redox-controlled preservation of a Mediterranean sapropel. *Nature Geoscience*, 1: 606-610.
- de Sousa A.A., Beaudet A., Calvey T., Bardo A., Benoit J., Charvet C.J., Dehay C., Gómez-Robles A., Gunz P., Heuer K., van den Heuvel M.P., Hurst S., Lauters P., Reed D., Salagnon M., Sherwood C.C., Ströckens F., Tawane M., Todorov O.S., Toro R. & Wei Y. (2023). From fossils to mind. *Communications Biology*, 6: 636.
- Devièse T., Stafford T.W., Waters M.R., Wathen C., Comeskey D., Becerra-Valdivia L. & Higham T. (2018). Increasing accuracy for the radiocarbon dating of sites occupied by the first Americans. *Quaternary Science Reviews*, 198: 171-180.
- Didier G., Fau M. & Laurin M. (2017). Likelihood of Tree Topologies with Fossils and Diversification Rate Estimation. *Systematic Biology*, 66: 964-987.
- Dietl G.P. & Flessa K.W. (2011). Conservation paleobiology: putting the dead to work. *Trends in Ecology & Evolution*, 26: 30-37.
- Dillon E.M., Pier J.Q., Smith J.A., Raja N.B., Dimitrijević D., Austin E.L., Cybulski J.D., De Entrambasaguas J., Durham S.R., Grether C.M., Halder H.S., Kocáková K., Lin C.-H., Mazzini I., Mychajliw A.M., Ollendorf A.L., Pimiento C., Regalado Fernández O.R., Smith I.E. & Dietl G.P. (2022). What is conservation paleobiology? Tracking 20 years of research and development. *Frontiers in Ecology and Evolution*, 10: 1031483.
- Dupuis C. (1984). Willi Hennig's Impact on Taxonomic Thought a Fascinating Epistemological Venture. *Annual Review of Ecology and Systematics*, 15: 1-24.
- Erba E., Bottini C., Weissert H.J. & Keller C.E. (2010). Calcareous Nannoplankton Response to Surface-Water Acidification Around Oceanic Anoxic Event 1a. *Science*, 329(5990): 428-432.

- Faurby S., Davis M., Pedersen R.Ø., Schowanek S.D., Antonelli A. & Svenning J.-C. (2018). PHYLLACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology*, 99: 2626.
- Fawcett T.W. & Higginson A.D. (2012). Heavy use of equations impedes communication among biologists. *Proceedings of the National Academy of Sciences*, 109: 11735-11739.
- Felice R.N. & Goswami A. (2018). Developmental origins of mosaic evolution in the avian cranium. *Proceedings of the National Academy of Sciences*, 115: 555-560.
- Felsenstein J. (1985). Phylogenies and the Comparative Method. *The American Naturalist*, 125: 1-15.
- Footo M. (2000). Origination and extinction components of taxonomic diversity: General problems. *Paleobiology*, 26: 74-102.
- Frenkel E. (2013). Don't Listen to E. O. Wilson. Math Can Help You in Almost Any Career. There's No Reason to Fear It. *Slate*, 60: 838. <https://www.ams.org/notices/201307/rmoti-p837.pdf>
- Gayon J. (2000). History of the Concept of Allometry. *American Zoologist*, 40: 748-758.
- Gee H. (2001). In search of deep time: Beyond the fossil record to a new history of life. 267 pp. Cornell University Press, Ithaca.
- Goswami A., Noirault E., Coombs E.J., Clavel J., Fabre A.-C., Halliday T.J.D., Churchill M., Curtis A., Watanabe A., Simmons N.B., Beatty B.L., Geisler J.H., Fox D.L. & Felice R.N. (2022). Attenuated evolution of mammals through the Cenozoic. *Science*, 378(6618): 377-383.
- Gould S.J. (1994). Tempo and mode in the macroevolutionary reconstruction of Darwinism. *Proceedings of the National Academy of Sciences*, 91: 6764-6771.
- Grün R. & Stringer C. (2023). Direct dating of human fossils and the ever-changing story of human evolution. *Quaternary Science Reviews*, 322: 108379.
- Gunz P. & Mitteroecker P. (2013). Semilandmarks: A method for quantifying curves and surfaces. *Hystrix*, 24: 103-109.
- Gunz P., Mitteroecker P., Neubauer S., Weber G.W. & Bookstein F.L. (2009). Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution*, 57: 48-62.
- Gunz P., Neubauer S., Maureille B. & Hublin J.-J. (2010). Brain development after birth differs between Neanderthals and modern humans. *Current Biology*, 20: R921-2.
- Harmon L.J., Weir J.T., Brock C.D., Glor R.E. & Challenger W. (2008). GEIGER: investigating evolutionary radiations. *Bioinformatics*, 24: 129-131.
- Hay W.W. & Sandberg P.A. (1967). The Scanning Electron Microscope, a Major Break-through for Micropaleontology. *Micropaleontology*, 13: 407-418.
- Henry A.G., Ungar P.S., Passey B.H., Sponheimer M., Rossouw L., Bamford M., Sandberg P., de Ruiter D.J. & Berger L. (2012). The diet of *Australopithecus sediba*. *Nature*, 487(7405): 90-93.
- Higham T. (2011). European Middle and Upper Palaeolithic radiocarbon dates are often older than they look: problems with previous dates and some remedies. *Antiquity*, 85: 235-249.
- Hone D.W.E. & Benton M.J. (2005). The evolution of large size: How does Cope's Rule work? *Trends in Ecology and Evolution*, 20: 4-6.
- Huelsenbeck J.P. & Ronquist F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17: 754-755.
- Kiessling W., Raja N.B., Roden V.J., Turvey S.T. & Saue E.E. (2019). Addressing priority questions of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374: 20190222.
- Kiessling W., Smith J.A. & Raja N.B. (2023). Improving the relevance of paleontology to climate change policy. *Proceedings of the National Academy of Sciences*, 120: e2201926119.
- Kuhn T.S. (1997). The structure of scientific revolutions. 242 pp. University of Chicago Press, Chicago.
- Kurtz J. (2023). The Bone Wars: The True Story of an Epic Battle to Find Dinosaur Fossils. 40 pp. Simon and Schuster, New York.
- Lang M., Binder M., Richter J., Schratz P., Pfisterer F., Coors S., Au Q., Casalicchio G., Kotthoff L. & Bischl B. (2019). mlr3: A modern object-oriented machine learning framework in R. *Journal of Open Source Software*, 4: 1903.
- Liu X., Jiang S., Wu R., Shu W., Hou J., Sun Y., Sun J., Chu D., Wu Y. & Song H. (2023). Automatic taxonomic identification based on the Fossil Image Dataset (>415,000 images) and deep convolutional neural networks. *Paleobiology*, 49: 1-22.
- Lösel P.D., van de Kamp T., Jayme A., Ershov A., Faragó T., Pichler O., Tan Jerome N., Aadepe N., Bremer S., Chilingaryan S.A., Heethoff M., Kopmann A., Odar J., Schmelzle S., Zuber M., Wittbrodt J., Baumbach T. & Heuveline V. (2020). Introducing Biomedisa as an open-source online platform for biomedical image segmentation. *Nature Communications*, 11: 5577.
- Lösel P.D., Monchanin C., Lebrun R., Jayme A., Relle J.J., Devaud J.-M., Heuveline V. & Lihoreau M. (2023). Natural variability in bee brain size and symmetry revealed by micro-CT imaging and deep learning. *PLOS Computational Biology*, 19: e1011529.
- Louca S. & Pennell M.W. (2020). Extant timetrees are consistent with a myriad of diversification histories. *Nature*, 580(7804): 502-505.
- Malanoski C.M., Farnsworth A., Lunt D.J., Valdes P.J. & Saue E.E. (2024). Climate change is an important predictor of extinction risk on macroevolutionary timescales. *Science*, 383(6687): 1130-1134.
- Maliet O., Hartig F. & Morlon H. (2019). A model with many small shifts for estimating species-specific diversification rates. *Nature Ecology and Evolution*, 3: 1086-1092.
- Marchant R., Tetard M., Pratiwi A., Adebayo M. & de Garidel-Thoron T. (2020). Automated analysis of foraminifera fossil records by image classification using a convolutional neural network. *Journal of Micropaleontology*, 39: 183-202.
- Marret F. (2023). The impact of artificial intelligence systems in micropaleontology. *Evolving Earth*, 1: 100022.
- Martins E.P. & Hansen T.F. (1997). Phylogenies and the Comparative Method: A General Approach to Incorporating Phylogenetic Information into the Analysis of Interspecific Data. *The American Naturalist*, 149: 646-667.
- Matthews T.J., Triantis K.A., Wayman J.P., Martin T.E., Hume J.P., Cardoso P., Faurby S., Mendenhall C.D., Dufour P., Rigal F., Cooke R., Whittaker R.J., Pigot A.L., Thébaud C., Jørgensen M.W., Benavides E., Soares F.C., Ulrich W., Kubota Y., Sadler J.P., Tobias J.A. & Sayol F. (2024). The global loss of avian functional and phylogenetic diversity from anthropogenic extinctions. *Science*, 386(6717): 55-60.
- McNamara K.J., Yu F. & Zhiyi Z. (2006). Ontogeny and heterochrony in the early Cambrian oryctocephalid trilobites *Changaspis*, *Duyunaspis* and *Balangia* from China. *Palaeontology*, 49: 1-19.
- Melchionna M., Castiglione S., Girardi G., Serio C., Esposito A., Mondanaro A., Profico A., Sansalone G. & Raia P. (2024). RRmorph—a new R package to map phenotypic evolutionary rates and patterns on 3D meshes. *Communications Biology*, 7: 1009.
- Micheli P. & Torre D. (1965). Riconoscimento e descrizione di una nuova specie del sottogenere *Grandarca*. *Palaeontographia Italica*, 60: 131-144.
- Mitteroecker P., Gunz P. & Bookstein F.L. (2005). Heterochrony and geometric morphometrics: A comparison of cranial growth in *Pan paniscus* versus *Pan troglodytes*. *Evolution and Development*, 7: 244-258.
- Mondanaro A., Di Febbraro M., Melchionna M., Maiorano L., Di Marco M., Edwards N.R., Holden P.B., Castiglione S., Rook L. & Raia P. (2021). The role of habitat fragmentation in Pleistocene megafauna extinction in Eurasia. *Ecography*, 44: 1619-1630.
- Mondanaro A., Di Febbraro M., Castiglione S., Melchionna M., Serio C., Girardi G., Belfiore A.M. & Raia P. (2023). ENphylo: A new method to model the distribution of extremely rare species. *Methods in Ecology and Evolution*, 14: 911-922.

- Morlon H. (2014). Phylogenetic approaches for studying diversification. *Ecology Letters*, 17: 508-525.
- Morris C., Mwaura N., Schneider D., Tabish F., Carpenter D., Clark N. & Sandip A. (2023). Graphics Processing Units' Accelerated Navier-Stokes Solvers for Unstructured Meshes: A Literature Review. *Proceedings of the ASME 2023 International Mechanical Engineering Congress and Exposition*. Volume 11: Mechanics of Solids, Structures and Fluids. New Orleans, Louisiana, USA: V011T12A016.
- Muhlbacher T., Piringner H., Gratzl S., Sedlmair M. & Streit M. (2014). Opening the Black Box: Strategies for Increased User Involvement in Existing Algorithm Implementations. *IEEE Transactions on Visualization and Computer Graphics*, 20: 1643-1652.
- Neubauer S. & Hublin J.-J. (2012). The Evolution of Human Brain Development. *Evolutionary Biology*, 39: 568-586.
- Neubauer S., Gunz P. & Hublin J.-J. (2009). The pattern of endocranial ontogenetic shape changes in humans. *Journal of Anatomy*, 215: 240-255.
- Neubauer S., Hublin J.-J. & Gunz P. (2018). The evolution of modern human brain shape. *Science Advances*, 4: ea05961.
- Nogués-Bravo D., Rodríguez-Sánchez F., Orsini L., de Boer E., Jansson R., Morlon H., Fordham D.A. & Jackson S.T. (2018). Cracking the Code of Biodiversity Responses to Past Climate Change. *Trends in Ecology and Evolution*, 33: 765-776.
- Nolan C., Overpeck J.T., Allen J.R.M., Anderson P.M., Betancourt J.L., Binney H.A., Brewer S., Bush M.B., Chase B.M., Cheddadi R., Djamali M., Dodson J., Edwards M.E., Gosling W.D., Haberle S., Hotchkiss S.C., Huntley B., Ivory S.J., Kershaw A.P., Kim S.-H., Latorre C., Leydet M., Lezine A.-M., Liu K.-B., Liu Y., Lozhkin A.V., Mcglone M.S., Marchant R.A., Momohara A., Moreno P.I., Müller S., Otto-Bliesner B.L., Shen C., Stevenson J., Takahara H., Tarasov P.E., Tipton J., Vincens A., Weng C., Xu Q., Zheng Z. & Jackson S.T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, 361(6405): 920-923.
- O'Meara B.C. & Beaulieu J.M. (2024). Noise leads to the perceived increase in evolutionary rates over short time scales. *PLOS Computational Biology*, 20: e1012458.
- O'Raifeartaigh C., O'Keeffe M., Nahm W. & Mitton S. (2017). Einstein's 1917 static model of the universe: a centennial review. *The European Physical Journal H*, 42: 431-474.
- Orlando L. & Cooper A. (2014). Using ancient DNA to understand evolutionary and ecological processes. *Annual Review of Ecology, Evolution, and Systematics*, 45: 573-598.
- Pääbo S. (1985). Molecular cloning of Ancient Egyptian mummy DNA. *Nature*, 314(6012): 644-645.
- Pandolfi L., Raia P., Fortuny J. & Rook L. (2020). Editorial: Evolving Virtual and Computational Paleontology. *Frontiers in Earth Science*, 8: 591813.
- Paradis E. & Schliep K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35: 526-528.
- Pichler M. & Hartig F. (2023). Machine learning and deep learning. A review for ecologists. *Methods in Ecology and Evolution*, 14: 994-1016.
- Piras P., Profico A., Pandolfi L., Raia P., Di Vincenzo F., Mondanaro A., Castiglione S. & Varano V. (2020). Current Options for Visualization of Local Deformation in Modern Shape Analysis Applied to Paleobiological Case Studies. *Frontiers in Earth Science*, 8: 00066.
- Piva A., Raimondi L., Rasca E., Kozmany A. & De Matteis M. (2024). A machine learning application for the automatic recognition of planktonic foraminifera in thin sections. *Marine and Petroleum Geology*, 166: 106911.
- Profico A., Buzi C., Davis C., Melchionna M., Veneziano A., Raia P. & Manzi G. (2019). A New Tool for Digital Alignment in Virtual Anthropology. *The Anatomical Record*, 302: 1104-1115.
- Profico A., Buzi C., Melchionna M., Veneziano A. & Raia P. (2020). Endomaker, a new algorithm for fully automatic extraction of cranial endocasts and the calculation of their volumes. *American Journal of Physical Anthropology*, 172: 511-515.
- Profico A., Buzi C., Castiglione S., Melchionna M., Piras P., Veneziano A. & Raia P. (2021). Arothron: An R package for geometric morphometric methods and virtual anthropology applications. *American Journal of Physical Anthropology*, 176: 144-151.
- Rabosky D.L. (2010). Extinction rates should not be estimated from molecular phylogenies. *Evolution*, 64: 1816-1824.
- Rabosky D.L. (2014). Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE*, 9: e89543.
- Raia P., Carotenuto F., Eronen J.T. & Fortelius M. (2011). Longer in the tooth, shorter in the record? The evolutionary correlates of hypsodonty in Neogene ruminants. *Proceedings of the Royal Society B: Biological Sciences*, 278: 3474-3481.
- Raia P., Carotenuto F., Passaro F., Fulgione D. & Fortelius M. (2012). Ecological specialization in fossil mammals explains Cope's rule. *American Naturalist*, 179: 328-337.
- Raia P., Mondanaro A., Melchionna M., Di Febbraro M., Diniz-Filho J.A.F., Rangel T.F., Holden P.B., Carotenuto F., Edwards N.R., Lima-Ribeiro M.S., Profico A., Maiorano L., Castiglione S., Serio C. & Rook L. (2020). Past Extinctions of *Homo* Species Coincided with Increased Vulnerability to Climatic Change. *One Earth*, 3: 480-490.
- Revell L.J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3: 217-223.
- Rohlf J.F. & Marcus L.F. (1993). A revolution morphometrics. *Trends in Ecology & Evolution*, 8: 129-132.
- Ruan J., Timmermann A., Raia P., Yun K.-S., Zeller E., Mondanaro A., Di Febbraro M., Lemmon D., Castiglione S. & Melchionna M. (2023). Climate shifts orchestrated hominin interbreeding events across Eurasia. *Science*, 381(6658): 699-704.
- Saltré F., Chadoeuf J., Peters K.J., McDowell M.C., Friedrich T., Timmermann A., Ulm S. & Bradshaw C.J.A. (2019). Climate-human interaction associated with southeast Australian megafauna extinction patterns. *Nature Communications*, 10: 5311.
- Sanderson M.J. & Donoghue M.J. (1994). Shifts in diversification rate with the origin of angiosperms. *Science*, 264(5165): 1590-1593.
- Sansalone G., Profico A., Wroe S., Allen K., Ledogar J., Ledogar S., Mitchell D.R., Mondanaro A., Melchionna M., Castiglione S., Serio C. & Raia P. (2023). *Homo sapiens* and Neanderthals share high cerebral cortex integration into adulthood. *Nature Ecology & Evolution*, 7: 42-50.
- Saupe E.E., Qiao H., Hendricks J.R., Portell R.W., Hunter S.J., Soberón J. & Lieberman B.S. (2015). Niche breadth and geographic range size as determinants of species survival on geological time scales. *Global Ecology and Biogeography*, 24: 1159-1169.
- Schlager S., Profico A., Di Vincenzo F. & Manzi G. (2018). Retrodeformation of fossil specimens based on 3D bilateral semi-landmarks: Implementation in the R package "Morpho." *PLoS ONE*, 13: e0194073.
- Sepkoski J.J. (1998). Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353: 315-326.
- Sepkoski J.J. Jr, Bambach R.K., Raup D.M. & Valentine J.W. (1981). Phanerozoic marine diversity and the fossil record. *Nature*, 293(5832): 435-437.
- Sheets H.D. & Zelditch M.L. (2013). Studying ontogenetic trajectories using resampling methods and landmark data. *Hystrix*, 24: 67-73.
- Silvestro D., Schnitzler J. & Zizka G. (2011). A Bayesian framework to estimate diversification rates and their variation through time and space. *BMC Evolutionary Biology*, 11: 311.
- Silvestro D., Salamin N. & Schnitzler J. (2014). PyRate: a new program to estimate speciation and extinction rates from incomplete fossil data. *Methods in Ecology and Evolution*, 5: 1126-1131.

- Silvestro D., Castiglione S., Mondanaro A., Serio C., Melchionna M., Piras P., Di Febraro M., Carotenuto F., Rook L. & Raia P. (2020). A 450 million years long latitudinal gradient in age-dependent extinction. *Ecology Letters*, 23: 439-446.
- Simpson G.G., Roe A. & Lewontin R.C. (2003). Quantitative zoology. 440 pp. Courier Corporation, San Diego.
- 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 Neanderthal mother and a Denisovan father. *Nature*, 561(7721): 113-116.
- Sokal A.D. (2000). The Sokal hoax: The sham that shook the academy. 271 pp. University of Nebraska Press, Lincoln.
- Soria C.D., Pacifici M., Di Marco M., Stephen S.M. & Rondinini C. (2021). COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. *Ecology*, 102: e03344.
- Sponheimer M., Alemseged Z., Cerling T.E., Grine F.E., Kimbel W.H., Leakey M.G., Lee-Thorp J.A., Manthi F.K., Reed K.E., Wood B.A. & Wynn J.G. (2013). Isotopic evidence of early hominin diets. *Proceedings of the National Academy of Sciences of the United States of America*, 110: 10513-10518.
- Stadler T. (2011). Mammalian phylogeny reveals recent diversification rate shifts. *Proceedings of the National Academy of Sciences of the United States of America*, 108: 6187-6192.
- Stewart M., Carleton W.C. & Groucutt H.S. (2021). Climate change, not human population growth, correlates with Late Quaternary megafauna declines in North America. *Nature Communications*, 12: 965.
- Tafforeau P., Boistel R., Boller E., Bravin A., Brunet M., Chaimanee Y., Cloetens P., Feist M., Hoszowska J., Jaeger J.-J., Kay R.F., Lazzari V., Marivaux L., Nel A., Nemoz C., Thibault X., Vignaud P. & Zable S. (2006). Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. *Applied Physics A*, 83: 195-202.
- Thompson D.W. (1917). On growth and form. 793 pp. Cambridge University Press, Cambridge.
- Timmermann A., Raia P., Mondanaro A., Zollikofer C.P.E., Ponce de León M., Zeller E. & Yun K.-S. (2024). Past climate change effects on human evolution. *Nature Reviews Earth & Environment*, 5: 701-716.
- Title P.O. & Rabosky D.L. (2019). Tip rates, phylogenies and diversification: What are we estimating, and how good are the estimates? *Methods in Ecology and Evolution*, 10: 821-834.
- Torre D. (1965). On the use of linear measurements in multivariate analyses applied to taxonomy. *Rivista Italiana di Paleontologia e Stratigrafia*, 71: 1271-1273.
- Walker S.E. (2023). Conservation biology and conservation paleobiology meet the Anthropocene together: history matters. *Frontiers in Earth Science*, 11: 1166243.
- Weber G.W. (2015). Virtual Anthropology. *American Journal of Physical Anthropology*, 156(S59): 22-42.
- Wilson E.O. (2013). Great Scientist  $\neq$  Good at Math. E.O. Wilson Shares a Secret: Discoveries Emerge from Ideas, Not Number-Crunching. *Slate*, 60: 837-838.
- Wingard G.L., Schneider C., Dietl G.P. & Fordham D. (2024). Turning Setbacks into Stepping-stones for Growth in Conservation Paleobiology. *Frontiers in Ecology and Evolution*, 12: 1384291.
- Xu Y., Liu X., Cao X., Huang C., Liu E., Qian S., Liu X., Wu Y., Dong F., Qiu C.-W., Qiu J., Hua K., Su W., Wu J., Xu H., Han Y., Fu C., Yin Z., Liu M., Roepman R., Dietmann S., Virta M., Kengara F., Zhang Z., Zhang L., An T., Zhang B., He X., Cong S., Liu X., Zhang W., Lewis J.P., Tiedje J.M., Wang Q., An Z., Wang F., Zhang L., Huang T., Lu C., Cai Z., Wang F. & Zhang J. (2021). Artificial intelligence: A powerful paradigm for scientific research. *The Innovation*, 2: 100179.
- Yang H., Butler E.R., Monier S.A., Teubl J., Fenyö D., Ueberheide B. & Siegel D. (2021). A predictive model for vertebrate bone identification from collagen using proteomic mass spectrometry. *Scientific Reports*, 11: 10900.
- Zhang Y., Feng H., Zhao Y. & Zhang S. (2024). Exploring the Application of the Artificial-Intelligence-Integrated Platform 3D Slicer in Medical Imaging Education. *Diagnostics*, 14: 146.
- Žliobaitė I. (2024). Laws of macroevolutionary expansion. *Proceedings of the National Academy of Sciences*, 121: 2314694121.
- Žliobaitė I., Fortelius M. & Stenseth N.C. (2017). Reconciling taxon senescence with the Red Queen's hypothesis. *Nature*, 552(7683): 92-95.
- Zollikofer C.P.E., Ponce de León M.S., Lieberman D.E., Guy F., Pilbeam D., Likius A., Mackaye H.T., Vignaud P. & Brunet M. (2005). Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature*, 434(7034): 755-759.

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