

Scanning the fossil record: stratophenomics and the generation of primary evolutionary-ecological data

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Abstract The amount and quality of paleontological data is rapidly increasing thanks to the new developments in geological dating, 3D visualization and morphometrics, chemical and histological analysis, and database storage. However, despite the fact that data from fossils, their assemblages, temporal successions, spatial gradients and environments are of an evolutionary-ecological nature, their contribution to current mainstream evolutionary-ecological theory and methodology is low. The use of fossils is not seldom restricted to calibration (e.g., in phylogenetics), or source for historical speculation after having analyzed modern data first (e.g., in macroecology). Yet, the scale of resolution of many paleontological time series (10^3 – 10^5 years) is highly apt for studying the dynamics of species, the average lifetime of which is in the order of 10^6 – 10^7 years. In order to fully profit from the wealth of data from the rock archive, a large-scale “stratophenomics” approach is needed. The resulting data archives will not only further contribute to an increase in the knowledge of past species, communities and environments, but will also generate more and innovative theory on the mechanisms underlying species and higher taxon dynamics. Examples of new and promising approaches towards generating paleontological data will be presented under the headings of the three major stratophenomics dimensions: time, morphology and environment. Highlighted fields include astrochronology, sclerochronology and 3D morphometrics.

Keywords Paleontology · Stratigraphy · Evolution · Macroecology · Stratophenomics · Morphometrics

Introduction

The field of paleontology is witnessing a silent but remarkable transformation. Interestingly, the nature of this shift is not so much taking place at the conceptual level, but rather

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at the level of primary data generation. One has only to visit paleontological meetings and sessions to be impressed by the increasing number of applications of 3D computer technology, high-resolution histology and chemistry on the one hand, and by the application of vast spatiotemporal databases on the other hand. In addition, more and more studies tune into the exciting new developments in geology with regard to high-resolution stratigraphy and environmental reconstruction.

The development towards the generation of vast amounts of high-quality primary historical data contrasts with the way the general public as well as the scientific community (including many biologists and geologists) perceive paleontology as a science. Undoubtedly, large shares of attention surrounding spectacular discoveries (dinosaurs, mass extinctions, “missing links”, etc.) are benefiting the field. On the other hand, the role of paleontology as a generator of enormous amounts of ‘mainstream’ spatiotemporal observations on organisms, populations, species and higher taxa is often too little known. Such observations clearly belong to the realm of evolution and ecology, but their role in current evolutionary biological and ecological theory and methodology is nonetheless relatively minor. Psychology is playing a role as well, as the effect of very use of the prefix —*palaeo* on non-specialists cannot be underestimated: the connotation with “museum stuff” is very strong, as is its homogenizing power of blurring long series of geological time intervals, each of which characterized by specific floras and faunas, into one notion of “old” or a few episodes at most (Rull 2010).

Obviously, fossil evidence is not evenly distributed. Some periods in Earth history are relatively better represented because they are represented by a larger volume of sedimentary rocks (Smith and McGowan 2005) or because these rocks are better suited to preserve fossils. Soft-bodied animal groups do hardly have a record. With the proper chemical (generally anoxic) conditions, however, organic materials may be preserved in detail. Extensive information on ecological and evolutionary events in terrestrial vegetation history can be inferred from numerous pollen and other paleobotanical records. Similarly, animal groups with hard parts may be amazingly well documented. For instance, the history of larger-sized invertebrates such as marine mollusks, echinoderms and arthropods and that of terrestrial vertebrates is well known at the global, regional and local scale. Marine microfossil communities constitute a still better potential for evolutionary-ecological study, because of their overwhelming availability in boreholes and uplifted land areas. Thus far, only a fraction of this material has been studied, the aim of research being mainly geological dating or climatic reconstruction. In addition, many paleontological datasets are suitable for studying community ecology, including the analysis of diversity and relative abundance patterns which can, with the appropriate corrections, be compared to their modern counterparts (Kidwell and Flessa 1996).

Although already a huge amount of information is housed in databases (for example, Paleobiology database: <http://paleodb.org/cgi-bin/bridge.pl>, Chronos-Neptune microfossil data base: <http://services.chronos.org/databases/neptune/index.html>, Pollen database <http://www.ncdc.noaa.gov/paleo/gpd.html>) many times more data are still scattered across the primary literature and collections, and this amount of evidence is again dwarfed by the data that are still residing in rocks. Although the accessibility of information on basic aspects such as taxonomic occurrence is rapidly growing, that of other relevant sorts of information such as relative abundances and morphology is still rather low. The same is true for accompanying information on environments as reconstructed from the physical and chemical properties of fossils and rocks, which often is not published directly in connection with the paleontological data. As in other disciplines, mandatory digital archiving of raw

data by journals further helps in disclosing large amounts of paleontological and geological information, which otherwise would have remained inaccessible (Callaway 2011).

Paleontology and evolutionary biology

Historically, *evolutionary biology* (definitions of which involves the origin, descent and change of species in time) has strong roots in paleontology. The geological record was pivotal for Charles Darwin in constructing his theory of evolution, although, slightly paradoxically, at the same time he stresses its shortcomings. In fact, the alleged completeness of the fossil record (Darwin 1859: Ch. 14) was a crucial point in order to maintain the notion of gradual organismic change, as it had been observed already by that time that fossil assemblages could rapidly change across rock series (see Eldredge 2006). The (often unjustified) idea that the fossil record is discontinuous and therefore unreliable appears to have left a mark in the minds of many biologists up to the present day. Recent analyses show that the fossil record is in fact quite well sampled in time (see Smith 2000), although completeness varies from place to place (Foote and Raup 1996). But even a relatively poor spatial resolution may not always be problematic when reconstructing the history of species, because the frequently time-averaged nature of fossil samples implies a more space-averaged (regional) signal as well.

The historical shift of focus in evolutionary biology towards studying present-day genes instead of past phenotypes is fully understandable, given the discoveries of Mendelian genetics, DNA structure and the subsequent spectacular developments in molecular biology. The marginalization of paleontology was already evident with the rise of the Modern Synthesis of the 1940s, to which paleontologist George Simpson's contribution basically was to show consistency with the mechanisms of natural selection and geographical speciation developed within other fields of biology. "Since that time the attitude of population geneticists towards paleontologists rash enough to offer a contribution to evolutionary theory has been to tell him to go away and find another fossil and not to bother the grownups" (Smith 1984). The theory of punctuated equilibria (Eldredge and Gould 1972) placed paleontology back in the spotlight as a field with own observations and theory, although controversies remained, for instance concerning the relative importance of clado- and anagenesis as evolutionary processes.

The peripheral contribution of paleontology with regard to evolutionary theory is not surprising, as paleontologists and evolutionary biologists do not actively communicate. Even when studying the same taxonomic groups, workers often present phylogenetic reconstructions in their own journals and meetings without taking into account the evidence from the other field. Nonetheless, the importance of fossil data for molecular phylogenetics is now gradually being accepted, as for instance evidenced by the pacing of relaxed molecular clocks by using multiple fossil calibration points (see Drummond et al. 2006). Evidently, optimal cross-fertilization takes place when geologically-dated occurrences are included into the analysis right from the start (e.g., Wilkinson et al. 2010), or when DNA from fossils themselves is addressed (only possible for maximally the last one million years ago, see Hadly et al. 2004 and Ramakrishnan and Hadly 2009 for examples of phylochronology, or the use of ancient DNA from stratigraphic series). Ideally, such analyses are accompanied by morphology-based phylogenetics of extinct groups, either with or without stratigraphic information directly included in the optimization criteria (Smith 2000).

Paleontologists have remained remarkably silent (but see for example Quental and Marshall 2010) on recent developments in taking molecular phylogenies a step further by using them for the study of diversification rates and radiations. Although the first studies in this direction were cautious, stressing the fact that molecular data only provide information on rates at which extant lineages give rise to other extant lineages (Nee et al. 1992), more recent writings go so far as to reconstruct actual historical events without taking extinct lineages into account (but e.g., see Magallón and Sanderson 2001, for an example of calculating diversification rates in angiosperms combining recent molecular and fossil morphological data). By including only recent taxa in calculating diversification rates in mammals (e.g., Bininda-Emonds et al. 2007; Stadler 2011) in fact only a small part of the lineages are used (given the average lifetime of mammal lineages of ~ 2.5 Myr, e.g., Alroy 2000). The same type of bias applies to recent molecular-based analyses for angiosperms, given the observation that the vast majority of the representatives do not belong to extant clades (Friis et al. 2005). Although modeling of extinction and speciation rates (Stadler 2011 among others) may compensate for the reduced amount of lineages in a general way, it never will allow the reconstruction of the actual historical events. The reason for this is the typical paleontological observation that the phylogenetic structure of major taxa most often consists of series of smaller clades successively replacing each other. The existence of such a pattern underlines the importance of paleontological data for evolutionary (and ecological) theory, as the actual mechanisms for clade and ecosystem replacements can only be learned from the paleontological and associated geological archives themselves (for example, Vrba 1995).

Apart from macroevolutionary studies focusing on the dynamics of species and higher taxa, paleontological records are also highly relevant for studies of microevolutionary (morphological) change within lineages and communities. Especially when combined with paleoenvironmental reconstructions, both types of studies can address the highly relevant question of proportional contributions of biotic, abiotic and random factors to evolutionary-ecological change (Ivany 1996).

Paleontology, ecology and scale

Larger-scale spatiotemporal patterns in diversity, abundance, body size and other ecologically relevant features by definition belong to the realms of *macroecology* and *biogeography* (Brown 1995; Brown and Lomolino 1998). Nevertheless most macroecologists deal with present-day spatial patterns only, and not with temporal patterns or past spatial patterns, let alone temporal trends in spatial patterns (Harrington 2010). For example, many studies dealing with present-day diversity patterns treat time as a residual after having regressed diversity on modern variables (climate, topography, etc.) first. The fact that history deserves a more prominent role in such analyses is demonstrated by the fact that usually different sets of modern variables are found for different continents or regions (McGlone 1996; Hawkins et al. 2003, Ricklefs 2004). As in the case of phylogenetics (see above), the best way to understand such differences is to explicitly integrate paleontological and geological data into macroecological analyses. In addition, the structure of various existing ecological frameworks, for example that of neutral biodiversity theory (Hubbell 2001) lends itself well to integration with the fossil record (Rosindell et al. 2011).

The usefulness of a specific fossil data source depends on the evolutionary-ecological question asked and its associated spatiotemporal and taxonomic scale (Bennington et al. 2009). Linked to this change in scale is a shift in the predominance of certain classes of

mechanisms (abiotic, biotic) explaining changes in taxa and communities (Barnosky 2001). For example, because the well-known Sepkoski compendium of marine invertebrate genera (Sepkoski 2002) is a global data set with a coarse time resolution (mostly Stages, i.e., mean duration close to 10^7 year), only very general trends and extreme events occurring at scales approaching 10^8 year (such as mass extinctions) can be recognized. Despite the storage of an increasing amount of fossil data in data bases, a time resolution (i.e., binning) of 10^7 year of is currently still the maximum attainable for large-scale global analyses of genera across major episodes (Paleozoic, Phanerozoic, etc., see Alroy et al. 2008), because global-scale temporal ranges of a large part of the taxa are only approximately known (typically the Stage level). Zooming in on the history of individual continents or oceans, while still using all geographical fossil information available, lowers the temporal resolution of the data to about 10^6 year (e.g., Kennett et al. 1985; Alroy 1996; van Dam 2006). In such cases, the temporal scale still relates to larger-scale regional (for instance climatic or oceanographic) trends, whereas the spatial scale allows for the recognition of geographical gradients (diversity, body size and other aspects of community structure) that can be compared to modern patterns. Mapping of distributions and other parameters is possible after choosing the appropriate temporal scale, with the highest temporal resolutions up to 10^3 year (e.g., pollen) attained for the latest Pleistocene to Holocene (for examples see Bennett 1990).

Finally, paleontological studies using the stratigraphic framework of an individual geological basin (subsided area filled with sediments) often involve temporal resolutions in the order of 10^3 – 10^5 year, although higher resolutions can be reached (Willis et al. 2010). The fossil samples themselves are usually time-averaged and represent durations of 10^2 – 10^4 year. Absolute chronological accuracy may reach 10^3 – 10^6 years depending on the dating method used, with higher accuracies being more common in the more recent geological past, particularly the late Pleistocene-Holocene. On the scale of a geological basin it is possible to actually trace local ecological communities, often across millions or tens of millions years of time (e.g., Turco et al. 2001; Barry et al. 2002; Tzedakis et al. 2006; van Dam et al. 2006; Ivany et al. 2009). On the other hand, the spatial data resolution associated with high-resolution temporal analyses will generally be lower, and in order to analyze or map trends across large basins or from basin to basin, data may have to be time-averaged once more. However, the loss of short-term variability need not to be problematic when focusing on larger scales, as time-averaged units of analysis often represent larger areas, and the temporal scale itself is appropriate for studying the origin, extinction and morphological trends of species, the average lifetime of which is in the order of 10^6 – 10^7 year.

Stratophenomics and its data sources

At various occasions, paleontologists have presented agendas of future (21st century) research (Jablonski 1999; Lane et al. 2000). Many topics have a global and large-scale temporal dimension, involving the study of massive extinctions and recoveries, responses to major perturbations, and key evolutionary innovations. Accordingly, practical aims revolve around the construction and use of databases with information pertaining to large spatiotemporal scales.

In the remainder of this paper I will focus on the smaller scale of successions of geological strata (the third scale mentioned above), and the morphology and chemistry of the fossil specimens they contain. In my opinion, a vital contribution of paleontology to

evolutionary and ecological theory lies in the compilation of large amounts of data at this scale. Such efforts cannot be seen in isolation from the development of new and sophisticated stratigraphic, morphometric and chemical methods, which in a certain sense allow a literal scanning of the record of past life.

In order to profit optimally from the rock-based archive during the coming decades an—omics type of approach is necessary, comparable to the genomics approach at the molecular level. An appropriate term describing the stratigraphic—morphological equivalent of genomics would be *stratophenomics*, a new concept which is introduced here to indicate the large-scale accumulation of quantitative data on the external shape, internal structure and taxonomy of fossils within the context of their communities, geological beds and associated past environments. Stratophenomics should not be confused with *stratophenetics*, which is a method of phylogenetic reconstruction using fossil sequences from time-ordered geological strata (Gingerich 1979). Another recently introduced term referring to larger-scale data collection using the fossil record is *ecometrics* (Eronen et al. 2010), which focuses on the compilation of functional morphological traits in both recent and fossil organisms. The main aim of ecometrics is the reconstruction of environments and climate using fossils, whereas stratophenomics aims to compile all types of quantitative information provided by fossils and their strata in order to reconstruct both their evolutionary and ecological history.

A selection of new developments with regard to primary data generation in paleontology will be presented below under the headings of the three major stratophenomic dimensions: time, morphology and environment.

Scanning time

The most influential recent advance in geochronology is undoubtedly *astrochronology*, a method of dating cyclical rock series that increases temporal accuracy and precision by an order of magnitude compared to previous methods. The method uses the now widely accepted notion that climatic oscillations of astronomical origin related to the direction and tilting of the axis of the Earth (precession and obliquity, respectively) and its orbit around the Sun (eccentricity) did not only control Quaternary glacial-interglacial alternations (Milankovitch 1920; Hays et al. 1976), but affected the Earth's climate throughout its history. These so-called Milankovitch cycles, which have primary periods of ~21 thousand years (precession), 41 thousand years (obliquity) and ~100 and ~400 thousand years (eccentricity), affect sedimentary sequences via insolation, climate and, among others, runoff, leaving their imprint as characteristic patterns as lithological alternations (orbital forcing). Once a suitable geological section (or drill hole) has been identified, one basically needs to compile a record of a well-measurable parameter (e.g., scans or recordings of fluctuating chemical element or mineral proportions, magnetic intensity, color properties, grain size, etc.) and perform spectral analysis to find periodicities.

Interaction between astronomers and geologists during the last 15 years has resulted in very precise calculations back 15 million years for the precession and obliquity of the Earth's axis and 40 million years for eccentricity (Laskar et al. 2004). Older rock series, such as those from the Mesozoic, show the same type of lithological patterns and have likewise been interpreted astrochronologically (for example, Olsen and Kent 1999). The resulting "floating" astrochronologies provide the same internal resolution and accuracy, but determination of numerical astronomical ages has to await incorporation into the "tuned" time scale that is extended continuously further back in time. This fundamentally new time scale, the Astronomical Time Scale (ATS, see Lourens et al. 2004) permits a

dating of stratigraphic and biological events about one order of magnitude better than previous time scales that depended mainly on radiometric and paleomagnetic dating alone (see also Hinnov 2004). What is more, the combination of the latter techniques with astronomical tuning allows for the astronomical age calibration of magnetic reversal boundaries (e.g., Hilgen 1991) as well as of standards used for radioisotopic dating (Ar/Ar dating: Kuiper et al. 2008).

In order to calibrate individual local geological successions unambiguously to the Astronomical Time Scale, generally long and continuous cyclic sections are needed. Because of non-uniform sedimentation rates that may even drop to or below zero (non-deposition and erosion, respectively) many sections are unsuitable for such a direct tuning. Nevertheless, bed alternation is a fundamental character of all sedimentary buildups, and given the rapidly increasing recognition in many different sedimentary environments, orbital forcing should be regarded as the null-model for explaining lithological alternations. In such cases, frequency ratios corresponding to known ratios between orbital periods could be used to generate hypotheses on orbital forcing. With the help of other stratigraphic and chronologic methods (magnetostratigraphy, radiometric dating, biostratigraphy) correlations to other well-dated sections elsewhere can be made, or at least hypotheses for the chronological and climatic control of the basic lithological alternations can be proposed.

What was not long ago regarded as an impossible task, the possibility to routinely perform regional or global “bed-to-bed” correlations with maximum uncertainties of 10,000 years (Fig. 1) within and even between the marine and continental realm has now become reality, also for the pre-Pleistocene (for instance, Van Vugt et al. 1998; Abels et al. 2009). Because the dating method allows precise chronological correlations across large distances, relatively short-lasting global climatic and environmental perturbations can be studied together with their effects on the biota. Moreover, because climate is the link between orbital motion and sedimentary expression, astronomical calibrations are directly

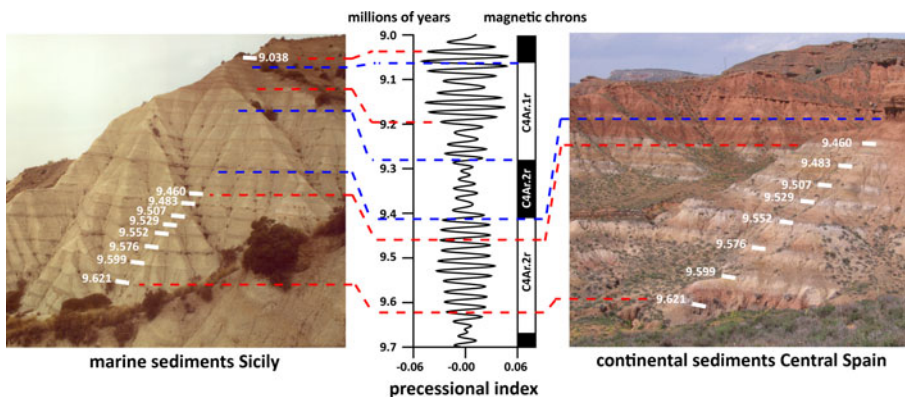


Fig. 1 Astrochronology and magnetostratigraphy of late Miocene sediments resulting in highly accurate dating of stratigraphic beds and their fossils. *Left* cyclic pattern of alternating light marls and dark sapropels (average cycle thickness $\sim 0.5\text{m}$) in marine sediments with microfossils in the Monte Gibliscemi section, Sicily (Hilgen et al. 2003; Hüsing et al. 2007); *right* cyclic pattern of alternating limestone and reddish and greenish clay-marl (average cycle thickness $\sim 2.5\text{m}$) in continental sediments with micromammal fossils in the Prado section, Teruel Basin, Spain (Abels et al. 2009). Both sections are tuned to the astronomical time scale for the Neogene (Lourens et al. 2004), and can be correlated “bed-by-bed”. *White lines* precession minima with ages, *red lines* astrochronological correlations, *blue lines* magnetostratigraphical correlations. Credit photographs: Frits Hilgen, Hemmo Abels

accompanied by climatic hypotheses, which then can be tested with the help of environmental proxy records (see below).

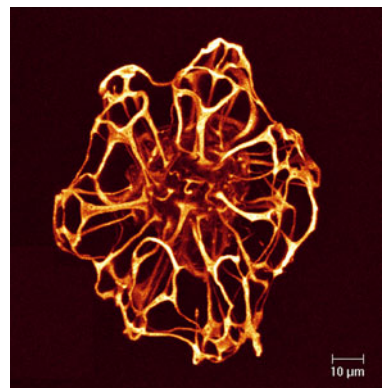
Scanning morphology

The increased availability of high-resolution 3D scanning equipment has created a new field called *virtual paleontology* (VP). High-resolution laser and (X-ray) computed tomography (CT) scanners can now routinely generate three-dimensional digital representations of the external and internal morphology across all organismic scales (Feist-Burkhardt and Pross 1999, see Fig. 2; Ketcham and Carlson 2001; Tafforeau et al. 2006; Lazzari et al. 2008). Software packages allow for subsequent manipulation and analysis of the 3D images, opening the door towards “fast-throughput morphometrics” (Evans et al. 2007; Smith and Strait 2008) in order to build up databases of specimens and mean population and species shapes (Fig. 2).

Paleontologists and other life scientists benefit in various ways from these developments. Firstly, taxonomic practice is revolutionized, because museum visits can be avoided and specimens need not to be touched or destroyed to view interior structures (e.g., Alba et al. 2010). Secondly, both classical and more sophisticated biometric measurements (such as area and volume calculations) as well as geometric morphometric studies in 3D can be carried out for systematic, functional morphological and phylogenetic purposes. Thirdly, biomechanical problems can be studied in a virtual way using the appropriate simulation and animation software. Nowadays such applications borrow from engineering by simulating stresses and strains to skeletal materials (Finite Element Analysis and Multimode Dynamics Analysis (Rayfield 2007; Curtis et al. 2008).

The marriage between VP and *Geometric Morphometrics* (GMM) is especially exciting, because, in contrast to classical morphometrics, GMM is explicitly taking within-specimen spatial relationships into account. It typically uses homologous landmark designs to first optimally superimpose specimens within and across populations or taxa to separate shape from size, and then apply multivariate ordination and grid or vector visualizations to analyze the results (Bookstein 1991; Rohlf and Marcus 1993; Slice 2007). Whereas most 3D (and 2D) applications deal with extant organisms, most of which are animals (but see Van der Niet et al. 2010), the number of paleontological applications is growing. The introduction of sliding ‘semi-landmarks’ in 2D and 3D (Bookstein 1997; Gunz et al. 2005) has proven to be an important advance to increase the number of landmarks along outlines and surfaces while still maintaining homologous relationships (see Fig. 3). Also for the

Fig. 2 Confocal laser image (3D reconstruction) of Middle Jurassic dinoflagellate cyst *Hapsidaulax margarethae*. Credit: Susanne Feist-Burkhardt. See also Feist-Burkhardt and Pross (1999) and <http://www.nhm.ac.uk/research-curation/research/projects/clsm/>



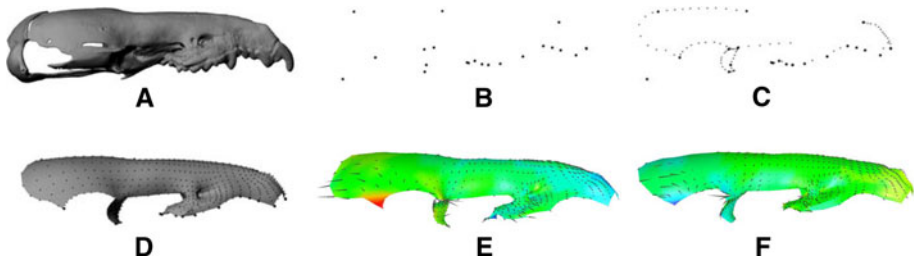


Fig. 3 Landmark-based geometric morphometrics of skulls of recent *Crocidura russula* (Soricidae, Mammalia) populations from France in right-lateral view. **a** Example of skull, **b** anatomical landmarks (39 in total, only partly visible); **c** curve semilandmarks (157 in total) with anatomical landmarks; **d** surface semi-landmarks (800 in total) with anatomical landmarks; **e** shape corresponding to lowest value of first principal component (*PCI*) of coordinates of aligned skulls, with arrows indicating relative deformation compared to mean shape in directions tangential to surface, and *colors* indicating directions normal to surface (*blue* inward, *red* outward, *green* intermediate); **f** as **e** but highest value of *PCI*. Modified from Souter et al. (2010): figures 2, 7 (reproduced with permission from Elsevier)

main alternative of landmark analysis, the Elliptic Fourier and Eigen shape analysis, 3D applications have appeared (Barrow et al. 2008; McPeck et al. 2008) thereby further extending on 2D outline analysis (for fossil examples see MacLeod 1999; Renaud and van Dam 2002; for a botanical example, see Jensen et al. 2002). For an overview of available GMM software packages is referred to <http://life.bio.sunysb.edu/morph/>.

For a long time it was thought that morphometrics and phylogenetics were relatively incompatible fields. This idea is largely incorrect: for instance, straightforward methods exist to use predefined phylogenetic trees to project shapes on to ancestors, to test for a phylogenetic signal and homoplasy in data, or to correct the variance in correlation and regression analysis in comparative studies (Rohlf 2001; Klingenberg and Gidaszewski 2009). The biggest current challenge is probably reconstructing phylogenies on the basis of continuous morphometric data (fossil and/or recent). Apart from the fact that significant shape information is lost, attempts to ‘discretize’ continuous geometric variation in order to run standard cladistic analyses have been launched with differential success (see discussions in Adams et al. 2004; Adams et al. 2011). On the other hand, modern versions of older algorithms for optimization of ancestor–descendant hypotheses using continuous data directly (distance- and likelihood-based methods, see Rohlf 2002; Catalano et al. 2010; Felsenstein 2004), have recently been implemented to landmark-based designs (Goloboff and Catalano 2010). Evidently, the true effectiveness of this class of promising methods can only be assessed after comparisons with known phylogenetic trees (see Klingenberg and Gidaszewski 2009).

Further future steps along these lines would involve stratigraphic constraints (as in standard cladistics, see Smith 2000) and developmental constraints (see Felsenstein 2002). The merging of morphometrics and phylogenetics with models of ontogenetic growth, especially those based known gene and protein expressions (Salazar-Ciudad and Jernvall 2010) could lead to truly ‘integrated evolutionary morphometrics’.

Scanning life history and environments

The study of chemical aspects of fossils has a long tradition, which is undoubtedly related to the close cooperation of paleontologists with geologists and geochemists interested in paleoenvironmental reconstructions. Both fossil and anorganic components from the

sediments are commonly used as so-called proxy records in geology (e.g., Totman Parrish 1998; Fischer and Wefer 1999). Apart from the study of distributions of major, minor and trace chemical elements and minerals, *stable isotope geochemistry* has proven to be exceptional powerful in reconstructing past environments, climate and ecology. For example, our current notion of the continuous alternation of cooling and warming episodes in the past has been shaped for an important part by the study of the distribution of ^{16}O and ^{18}O isotopes in the shell carbonate of marine microfossils such as foraminifera (Emiliani 1955; Zachos et al. 2001). A recent breakthrough in this field with regard to very precise temperature reconstructions constitutes the analysis of ^{13}C - ^{18}O bonds (or clumped isotopes, Ghosh et al. 2006). The isotopic compositions of other elements such as carbon, nitrogen, hydrogen, sulfur, strontium in biotic and abiotic components of terrestrial and marine sediments provide clues on key environmental changes such as those in aridity, CO_2 , primary productivity, ocean current patterns, altitude and continental weathering. Stable isotopes also inform about the ecology of taxa and entire communities, for example with regard to photosynthetic pathways (carbon isotopes in plants and animals, e.g., Koch 1998), migration patterns (strontium isotopes, e.g. Hoppe et al. 1999), and food webs (nitrogen isotopes, e.g., Post 2002).

A highly successful new development involves the combination of within-specimen chemical data with records of growth increments in fossil tissues. As a forerunner of growth structure research, *dendrochronology* has established itself as a discipline of its own, using tree rings in mainly sub-recent and sub-fossil wood remains to perform detailed age estimations and to reconstruct associated environments. Moreover, a rich literature has developed on combining the analysis of (sub-)tree ring width and density with stable carbon oxygen, and nitrogen stable isotope composition (see Robertson et al. 2008). Inspired by the results of dendrochronology, earth scientists have re-discovered *sclerochronology* (Buddemeier 1978), which is the study of growth increments in mineralized animal tissue. The recent sharp increase in sclerochronological studies on both fossil and living organisms (for calibration purposes), which is partly driven by the increased interest in the reconstruction of past climatic seasonality, is noteworthy (e.g., <http://www.paleontology.uni-mainz.de/ISC2010/>). It is now evident that growth structures in fossils of individual organisms such as shells and bones provide unique windows to past life histories and environments. The rhythms of organismic activity that can be observed in skeletal parts range from decadal (e.g., coral colonies) to annual, and further down to fine banding patterns that reflect differential activity during day and night (Figs. 4, 5). Such daily layering can then be used to identify other rhythms such as lunar cycles (for example, Schöne et al. 2007; see Fig. 4) or Lines of Arrested Growth (LARs) related to stress events (Klevezal. 1996; Macho et al. 2003, see Fig. 5; Köhler and Moyà-Solà 2009).

Conclusion

Although by its very nature the paleontological record is consisting of evolutionary-ecological data, the observed patterns in these data do not play an important role in current mainstream evolutionary-ecological theory. At the same time, the quality of paleontological and accompanying geological data sets is rapidly increasing thanks to new developments in 3D scanning and morphometrics, chemical and histological analysis, and geochronology. In order to fully profit from all available information from fossils and sediments in the near future, a large-scale “stratophenomics” approach is necessary. As a result, actual histories of populations, species, communities and environments will be

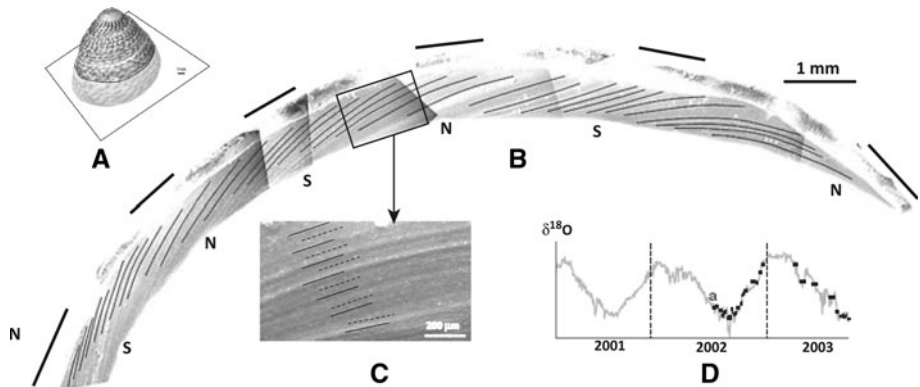


Fig. 4 Combined sclerochronological and stable isotope analysis of extant gastropod *Gibbula cineraria* from Helgoland, southern North Sea. **a** Sketch showing position of cut through last whorl; **b** Last one-third of last whorl corresponding to 5 weeks of growth after grounding, polishing and immersion. Most important growth lines indicated. Growth rates are higher during spring tide (*S* spring tide, *N* neap tide). *Thick black lines* indicate spots where shell carbonate was sampled for stable isotopes. **c** Detailed image with daily increments, which are subdivided into two increments which is typical for shells in the intertidal and shallow subtidal zone; **d** oxygen isotope composition as observed on shell (*black rectangles*) and predicted from water temperature and salinity (*grey line*). Modified after Schöne et al. (2007): figures 3, 7, 10 (reproduced with permission from Springer)

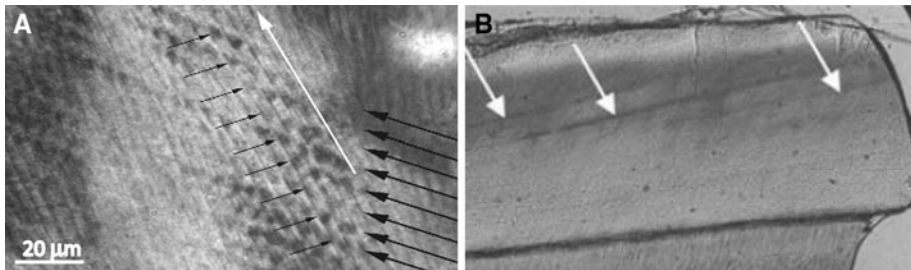


Fig. 5 **a** Staircase shaped laminations observed with transmitted light microscopy of sectioned tooth of Miocene rhinocerotid *Brachypotherium stehlini*. *Long white arrows* show directions of prisms. *Long black arrows* show daily laminations, which consist of aligned cross-striations (indicated by *short black arrows*) corresponding to individual enamel prisms (after Tafforeau et al. 2007; reproduced with permission from Elsevier); **b** Thin section of tooth cusp of the extant African grazing bovid *Alcelaphus buselaphus*, showing stress lines caused by metabolic disturbance that is probably related to seasonal food shortage (Macho et al. 2003; reproduced with permission from Elsevier)

much better known, key evolutionary-ecological patterns in species and higher taxa will be detected, with underlying mechanisms being much better understood.

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