General palaeontology

Biodiversity and evolution in the light of morphometrics: From patterns to processes

La biodiversité et l'évolution à la lumière de la morphométrie : des patterns aux processus

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A B S T R A C T

Disparity (shape diversity) is a key aspect of biodiversity, both present and past. The shapes of organisms are usually quantified by means of morphometrics. In this article, after a short review of recent advances and applications of morphometric methods, examples are presented as an overview of morphometric studies undertaken at the Biogéosciences research unit of Burgundy University. They concern both works on shape differentiation and evolution of disparity through time, and work aiming to infer, from the shapes of the organisms, any developmental stresses, constraints or processes which could explain in part the resulting disparity. The objective is to demonstrate how useful morphometrics can be for research in evolutionary and developmental biology.

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R É S U M É

La disparité (ou diversité des formes) est un aspect clé de la biodiversité actuelle et passée. La quantification de la forme des organismes s'effectue traditionnellement grâce à la morphométrie. Dans cet article, après une revue rapide des améliorations et des applications récentes des outils morphométriques, quelques exemples illustrant les études morphométriques menées au laboratoire Biogéosciences de l'université de Bourgogne sont présentés. Ils comprennent à la fois des travaux sur la différenciation des formes et l'évolution de la disparité au cours du temps, ainsi que des travaux visant à estimer des stress, contraintes ou processus du développement à partir de la forme des organismes, et pouvant être en partie responsables de la disparité résultante. L'objectif est de montrer l'utilité de la morphométrie pour des recherches en biologie évolutive et développementale.

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1. Introduction

Biodiversity, in its structural aspect (in complement with its functional one, i.e. relationships between species

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and their environment), can be described at three levels: population level (diversity of genes within a species), inter-specific level (diversity among species) and ecosystem level (diversity of species assemblages and communities). At the interspecific level, structural biodiversity can be estimated by specific richness, and by morphological diversity (also called disparity; for reviews on diversity and disparity, see e.g. Foote, 1997; Gotelli and Colwell, 2001). Specific rich-ness is likely to be the most known and most used proxy to assess species diversity, both extant and past. Diver-sity dynamics through geological time (including periods of extinction and radiation) is currently being described using various estimates of species richness. Disparity is also a rel-evant proxy to account for diversity changes through time; it provides useful tools to depict morphological changes and assesses the underlying processes. Disparity studies tackle different issues, including taxonomy, population differentiation, developmental constraints and ecological stresses, which are all relevant to shape analysis and evo-lution.

Prior to any disparity study, organism forms must be quantified to be compared: morphometrics is a set of tools precisely designed for this aim. For morphometricians, form usually encompasses size and shape, i.e. all geometric properties independent from size, position and orientation (see e.g. Klingenberg, 2010). These geometric properties include the whole shape of organisms, as well as the shape of parts of them (modules, discrete elements such as ver-tebrate bones or echinoderm plates), and the spatial arrays of these parts (patterns of topological relationships).

Morphometrics deals with shape analysis and shape variation (Bookstein, 1991) among specimens of a single population or among specimens of distinct populations (see Adams et al., 2004; Mitteroecker and Gunz, 2009; Slice, 2007 for the most recent reviews about development, application fields, and remaining challenges of morpho-metrics), and it is increasingly used for evolutionary studies (Fig. 1).

Historically, as a first morphometric approach or "traditional morphometrics" (also called "multivariate morphometrics"), shape has been described using a col-lection of linear measurements (mainly linear distances between body parts or extremities, ratios, angles, areas, volumes). Then measurement data were analysed using multivariate statistics. Although very simple to perform, traditional morphometrics suffers from several limitations (for an exhaustive list see Adams et al., 2004), notably the reconstruction of the original shape using measurement data is seldom possible.

Morphometrics underwent what Rohlf and Marcus, 1993 qualified as a "revolution" in the 1980s and 1990s, when a new field of morphometric studies called "mor-phometric geometrics" emerged. This field encompasses methods based on the description of shape outline using fitting functions (the most current are Fourier series, Rohlf, 1990), and on landmark coordinates (i.e. Procrustes align-ment of homologous landmarks configurations: Dryden and Mardia, 1998; Rohlf and Slice, 1990, and Thin Plate Spline deformation grids: Bookstein, 1991). The main advantage of those procedures is the possibility of return-ing to the original shape. Moreover, concerning Procrustes
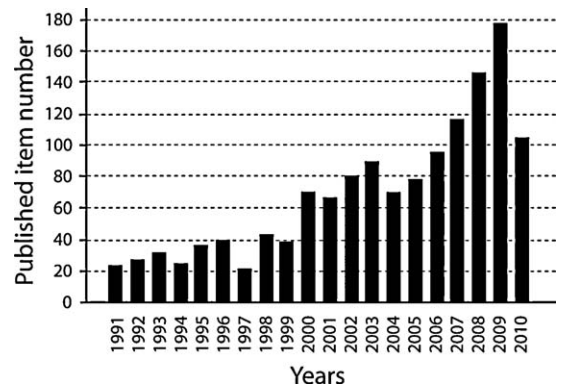

Fig. 1. Evolution through time of publication number using morphomet-rics for evolutionary studies. Data come from a query on the Web of Science database processed on 2010/08/24 (so the 2010 effective appar-ently low is only temporary), by searching all publications containing the words "morphometry" or "morphometric" or "morphometrics" in their topics, and by refining results to publications whose subject area is "evo-lutionary biology". Note the increasing trend.

Fig. 1. Évolution au cours du temps du nombre de publications utilisant la morphométrie dans le cadre d'études évolutives. Les données provi-ennent d'une requête effectuée le 24/08/2010 sur la base de données du Web of Science, en recherchant toutes les publications contenant les ter-mes « *morphometry* » ou « *morphometric* » ou « *morphometrics* » dans leur sujet (champ « *topic* »), et en affinant les résultats aux publications trai-tant de biologie évolutive (champ « *subject area* » restreint à « *evolutionary biology* »). Notez que la tendance augmente clairement.

and TPS methods, a robust theoretical framework of shape space was defined (Kendall, 1984; Rohlf, 1999; Slice, 2001). Sliding semilandmarks (Bookstein, 1997; Perez et al., 2006) make possible the description of shapes combining curves and classical homologous landmarks on the same object.

Enhancements, principally in the field of landmark-based methods, have increased the range of biological shapes that can be analyzed using morphometric geomet-rics:

- taking the third dimension into account in shape analysis is possible due to technical advances in data acquisi-tion (microscribes or CT scans, e.g. Specht et al., 2007; Tafforeau et al., 2006);
- procrustes analysis of shapes made of articulated parts is not hindered anymore by the motion of the different parts during data acquisition (Adams, 1999);
- methods have been developed to address the issue of missing landmarks (e.g. Gunz et al., 2009; Neeser et al., 2009; Strauss and Atanassov, 2006), which is quite a fre-quent situation in the study of fossils;
- several solutions have been proposed to assess the part of shape variations due to measurement error (Arnqvist and Martensson, 1998; von Cramon-Taubadel et al., 1997).

Frequently, morphometrics is used to address ques-tions concerning morphological evolution, for example by studying specific differentiation processes or by quantify-ing morphological disparity, through time and/or space. During the last two decades, the spectrum of the ques-tions addressed in morphometric studies has become broader, including (among others): developmental sta-bility assessed by directional and fluctuating asymmetry

(Klingenberg and McIntyre, 1998; Mardia et al., 2000; Palmer and Strobeck, 1986), relations between genes and morphology (e.g. Klingenberg and Leamy, 2001; Klingenberg et al., 2001; Monteiro et al., 2002), and the estimation of morphological integration and modularity (e.g. Cheverud, 1995; Klingenberg, 2010; Magwene, 2001; Mitteroecker and Bookstein, 2007). Another promising application of geometric morphometrics is the reconstruction of hypothetical ancestral morphologies based on molecular phylogenies and current morphologies (Wiley et al., 2005).

In this article, an overview of morphometric approaches and applications undertaken at Biogéosciences (Dijon, France) will be presented through several case studies. More than ten years after, it echoes to the paper by Neige et al. (1997) where a first overview of morphometric studies performed at Biogéosciences was given. This will provide a review of some of the new applications of morphometric studies.

2. Morphometrics and morphological differentiation

2.1. Case examples

The most classic and straightforward applications of morphometric approaches are (i) the study of shape differentiation between extant or past populations or species (e.g. Dommergues et al., 2006; Neige, 2003); and (ii) the quantification of shape disparity through time and/or geography (e.g. Dera et al., 2010; Lefebvre et al., 2006; Moyne and Neige, 2007). This quantification is performed by studying the occupation of a multivariate space, called "morphospace" (for a review on theoretical morphospaces, see Dera et al., 2008), resulting from multivariate analyses on shape variables. For extant data, morphological differentiation can be confronted to molecular or genetic differentiation, to know to what extent morphological evolution reflects genetic evolution (e.g. Garnier et al., 2005; Magniez-Jannin et al., 2000; Tougard et al., 2008). We evoke below some of the main results from two typical studies.

In the first example (Neige, 2003), the current biodiversity of more than one hundred of cuttlefishes (Sepiidae family) from 17 biogeographical units of the Old World is studied by means of two metrics: diversity (species richness) and disparity of cuttlebones (i.e. cuttlefish inner shells). Their shapes are quantified and compared by Procrustes methods on landmark data. One interesting result is the disconnection between diversity and disparity signals: a high number of species in a given biogeographic zone does not imply systematically high shape diversity and conversely. In two biogeographic zones (southern Africa and East India), this disconnection is particularly marked, and still remains to be explained, probably by improved knowledge of phylogenetic links between cuttlefish species.

The second example (Lefebvre et al., 2006) deals with the diversity of stylophores (i.e. atypical Paleozoic echinoderms) studied from the Middle Ordovician to the Early Silurian at the global scale. The morphological disparity of nearly 40 stylophoran species was measured by means of traditional morphometrics on plates and thecae, and

compared to the signals of diversity and of "palaeogeographic dispersion" (assessed by an index quantifying the geographic occupation by species). The main results are: (i) a dissociation of the diversity and disparity signals at the beginning of the stylophoran radiation (Middle Cambrian–Tremadocian), where the diversification of shapes precedes that of species and is reflected by the rapid but sparse occupation of the morphospace (Fig. 2); and (ii) the absence of relation between species and shape diversity, and palaeogeographic dispersion, suggesting that colonization of new habitats was not a prerequisite for stylophoran speciation and morphological differentiation.

In the two subsequent parts, we develop two promising approaches to study shape differentiation:

- by taking advantage of the very particular context of bioinvasions and the possibility of hybridations between close species (for this last point, see, for example, Renaud et al., 2009);
- by using graph theory to quantify morphological characters (contacts between plates of sea urchins) not describable by classic morphometric approaches.

2.2. Bio-invasions as promising models for the study of morphological diversification

If bio-invasions (or biological invasions), the recent spread of a species out of their native range, are one of the major threats for biodiversity, they also provide a unique opportunity to study evolutionary changes *in natura* over a contemporary timescale (Stockwell et al., 2003). Mainly during the last two decades, numerous studies have examined population genetics of invasive species and the evolution of phenotypic traits suspected to play a key role in their success (Lee, 2002). Morphological traits were also seen as powerful markers to detect translocated populations and to trace their biogeographic origins (e.g. Berrou et al., 2004). However, few workers focused on the morphological diversification that can emerge following a bioinvasion phenomenon. As with any phenotypic trait, rapid morphological changes during bioinvasions probably result from three non-exclusive evolutionary processes:

- *Random effects.* Invasive populations are often funded from a low number of individuals. Thus, founder effects and the subsequent genetic drifts before population expansion are supposed to have a deep impact on morphological divergence (see Kolbe et al., 2007 for a documented example on *Anolis* lizards);
- *Environmental effects.* Since invasive species frequently spread across a broad range of ecological conditions, correlations between environmental parameters and morphological variation are expected (see e.g. Collyer et al., 2005). In such a case, distinguishing the historical role of genetic effects and phenotypic plasticity, as well as understanding the functional significance of morphological variation are challenging issues;
- *Genetic admixture effects.* Hybridization and genetic introgression between populations or species are some of the major consequences of species introductions (Rhymer
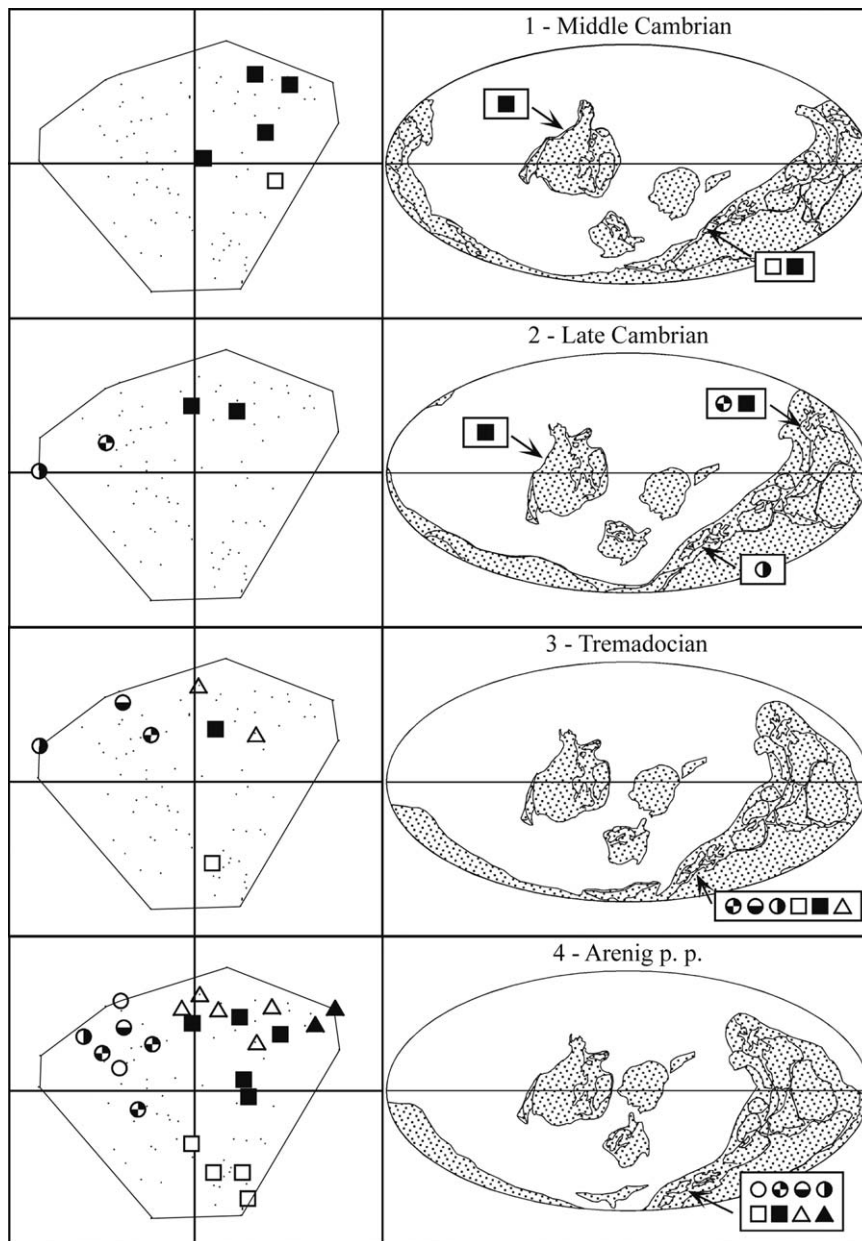
Fig. 2. Evolution through time (from the Middle Cambrian to the end of the Early Ordovician) of stylophoran morphospace occupation and paleogeographic dispersion (modified from Lefebvre et al., 2006). The symbols correspond to morphological subset identified by hierarchical clustering.

Fig. 2. Évolution temporelle (du Cambrien moyen à la fin de l'Ordovicien inférieur) de l'occupation de l'espace morphologique des stylophores et de leur dispersion paléogéographique (modifiée d'après Lefebvre et al., 2006). Les figurés correspondent à des groupes morphologiques identifiés par classification hiérarchique.

and Simberloff, 1996). In some cases, hybrid phenotypes can differ from parental ones, which can be responsible for a higher adaptive potential (Nolte et al., 2005).

These potential causes for morphological divergence during bio-invasions match those generally suggested to explain evolutionary diversifications (Schluter, 2000; Seehausen, 2004); and species invasions, seen as recent natural experiments, could allow morphologists to better discriminate their respective implications. Thus,

we suggest that a morphological approach to bio-invasions should represent a fruitful field of investigation: (i) to improve our understanding of the processes governing the emergence of morphological diversity over broader time and taxonomic scales; and (ii) to help us to highlight some dark sides of the mechanisms linking genotype and phenotype during the adaptation process.

An ongoing project focuses on one of the world's worst invasive species, the tilapia *Oreochromis mossambicus*. Nat-

urally restricted to few southern African rivers before the 1930 s, this cichlid fish is now introduced worldwide for aquaculture in tropical and subtropical continental waters. The large number of countries, islands and unconnected hydrological basins where *O. mossambicus* escaped and established itself in the wild, coupled with its abilities to survive in a broad range of ecological conditions (e.g. including gradients in salinity level, dissolved oxygen concentration, and predation pressures) (Canonico et al., 2005; Pérez et al., 2006), make this species an ideal candidate for the study of contemporary morphological evolution. In this context, a preliminary geometric morphometrics analysis of external body shape reveals significant divergence between populations introduced approximately 50 years ago. If *O. mossambicus* taken as a model species provides the opportunity to study the dynamics of drift and adaptation over a contemporary time scale, it also allows the appraisal of short-term consequences on morphological variation of introgressive hybridization in the wild. Indeed, *Oreochromis* species easily introgress once in contact with each other. The introduction of the related species *Oreochromis niloticus* in the Limpopo basin (South Africa and Mozambique) and the bio-invasion of the resulting *O. mossambicus* x *O. niloticus* hybrids (D'Amato et al., 2007) provide an exciting situation to highlight the interactions between a sudden increase in genetic variation and adaptation process in a strongly structured environment. Finally, the additional interest of *O. mossambicus* results from the rich background in genomics and developmental biology of *Oreochromis* (e.g. Fujimura and Okada, 2008; Lee et al., 2005), which should offer in the very near future the opportunity to tackle fundamental questions about the microevolution of development in order to better understand how environment acts on the genotype and on its expression to build up an integrated organism. As a second step, one can hope that the phylogenetic proximity of the *Oreochromis* genus with highly diverse African Cichlid species flocks (Schwarzer et al., 2009) will appear as a fruitful situation to fill some gaps between the microevolutionary process and the emergence of biodiversity.

2.3. Characterization of echinoid plate organization using graph theory

The shape aspect considered here is the spatial organization of elementary parts of organisms, quantified by means of graph theory. It concerns the study of mathematical structures used to model pairwise relations between objects from a certain collection. Many situations can conveniently be described using a diagram consisting of a set of points with lines connecting certain pairs of these points, and graph theory has been applied to many fields of interest, among which architecture (Baglivo and Graver, 1983), social and biological sciences (Samadi and Barberousse, 2006).

Graph theory has been very seldom applied to morphological studies of biological models, but Rasskin-Gutman (2003), and Rasskin-Gutman and Buscalioni (2001) exemplified morphological applications to vertebrates, using graphs as a tool for studying shape variations and evolution of pelvic girdles and skulls. In their case studies, the boundary pattern of each skeletal element was defined by the connection to other elements. As in vertebrates, the echinoderm skeleton consists of many elements (so-called plates or ossicles), the boundary patterns of which determine the whole shape of organs and are essential in systematics and related to main evolutionary events. In the case presented herein, we show how graph theory is a relevant tool for depicting and describing apical plate patterns of a well diversified sub-group of irregular echinoids: the Spatangoida. Shape variations are not analyzed for every single plate, but shape evolution of the whole structure is studied using graph theory.

Spatangoid echinoids originate at the dawn of the Cretaceous and have been the most diversified order of echinoids ever since, counting approximately 150 fossil genera and hundreds of species. In spatangoids, there are between six and nine apical plates – located at, or close to, the top of the test – that constitute the so-called apical system, a skeletal structure involved in biological functions such as reproduction, inner pressure control and growth (new plates form in close contact with certain well-defined apical plates during growth). Consequently, the boundary pattern of apical plates has always been a concern of systematicists, and the way this pattern has changed through time is a key to understanding echinoid evolution (Kier, 1974; Néraudeau, 2001; Saucède et al., 2004, 2007).

The extensive survey of drawings and figures published for half a century (e.g. Fischer, 1966; Kier, 1974; Mortensen, 1951; Néraudeau, 2001), along with our own observations led us to identify 24 different boundary patterns of apical plates in adult specimens of spatangoids, that is to say 24 different ways apical plates connect to each other, all apical plates considered (François, 2004). This is a very low number as compared to the 6.87×10^{10} different boundary patterns that can be constructed with nine elements and that correspond to the maximum number of possible patterns according to graph theory. Such low morphological diversity suggests very strong constraints. Among those constraints, the most pregnant comes from the fact that plates are physical entities with a given surface and cannot be totally freely organized. However, some others are inherited from the history of clades and bear a phylogenetic signal.

To describe and explore the disparity of spatangoid apical systems, boundary patterns of each type of apical system were symbolized in a graph, with plates coded as vertices and connections between plates as edges (Fig. 3A).

Preliminary results (François, 2004) show that:

- certain intraspecific and interspecific morphological variations may overlap, sometimes questioning systematics at the species and genus level;
- the strongest anatomical constraint is related to genital Plate 2 (G2 in Fig. 3) that tends to develop through time (Fig. 3B) and reduce the overall compactedness of the structure due to the loss of connections between plates (Fig. 3C). Compactedness can be reduced by the loss of genital plates too;
- disparity of apical patterns decreases with time as spatangoids become more derived.
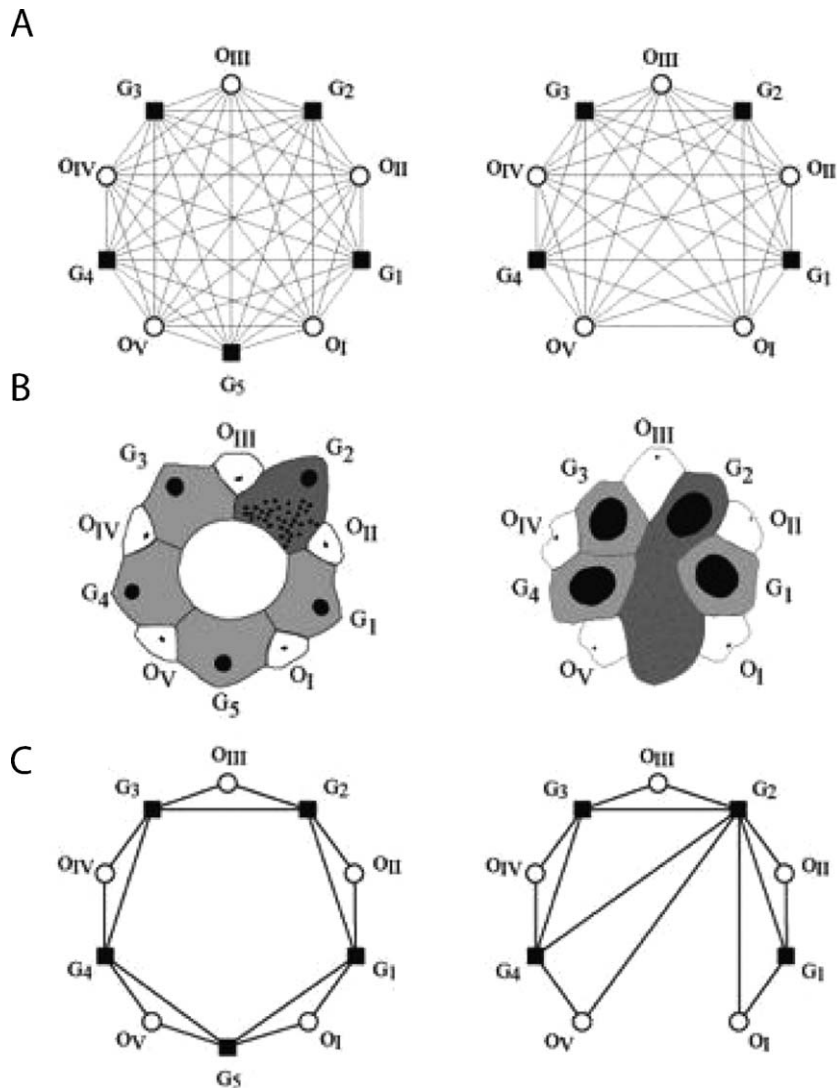
Fig. 3. A. Complete graph drawings for 10 (left) and 9 (right) vertices, showing the 45 and 36 possible edges respectively. **B.** Apical systems of a regular (left, with 10 plates) and spatangoid (right, with 9 plates) echinoid. O stands for ocular plates and G for genital plates. **C.** Graph drawings of actual connections between plates for the regular (left) and spatangoid (right) echinoid.

Fig. 3. A. Représentation des graphes complets pour 10 (à gauche) et 9 (à droite) sommets, montrant respectivement les 45 et 36 connexions théoriques possibles. **B.** Systèmes apicaux d'un échinide régulier (à gauche, avec 10 plaques) et d'un spatangue (à droite, avec 9 plaques). Les « O » correspondent aux plaques ocellaires et les « G » aux plaques génitales. **C.** Représentation des connexions réellement observées chez l'échinide régulier (à gauche) et le spatangue (à droite).

3. Morphometrics and development

The first applications of morphometric approaches to study organism development principally concerned characterization of allometries and heterochronies (David, 1990; Dommergues et al., 1986). Both can explain in some cases morphological variations within and among species (for interesting perspectives of the use of allometries in the assessment of morphological disparity, see Gerber et al., 2007, 2008). With the emergence of the evo-devo framework (for evolutionary developmental biology, i.e. the study of morphological evolution through developmental processes), morphometrics has found a fertile field of applications. In this part, we briefly review some examples of

morphological asymmetry studies, before detailing some results obtained on vole teeth.

3.1. Case examples

In symmetric structures (bilateral for most organisms), the observation of deviation from this symmetry can give valuable information on the developmental stability of organisms (i.e. the result of processes which resist perturbations affecting developmental trajectories -or buffer them- within a given environment). Several types of morphological right-left asymmetry are defined (see Palmer and Strobeck, 1986), and the levels of one of them, fluctuating asymmetry, may depend both on
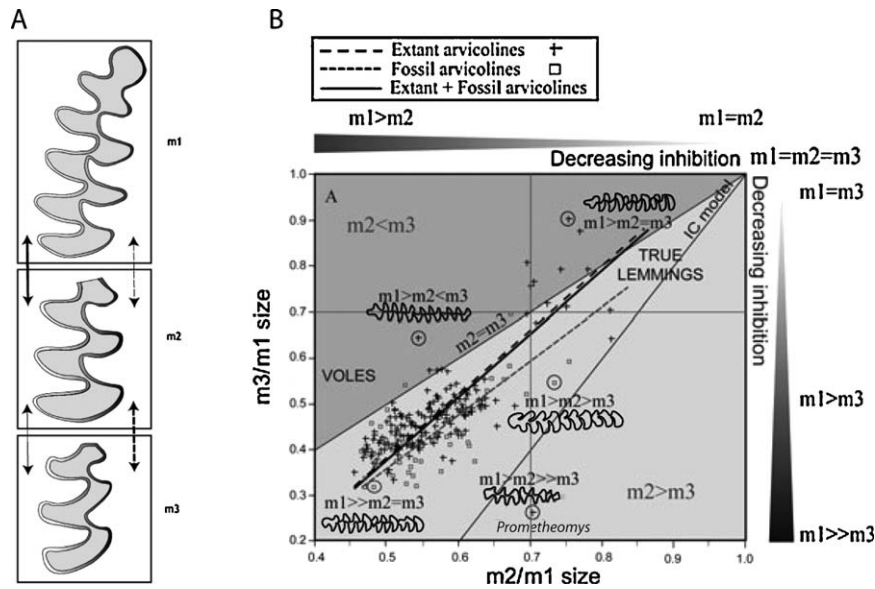
Fig. 4. A. Occlusal view of the lower molars (from m1 to m3) of *Microtus arvalis*, and schematic representation of modularity (black rectangles). Developmental processes responsible for modularity are symbolized by arrows, whose width indicates the degree of integration, and whose line type (continuous or dashed) symbolizes two different processes (from Laffont et al., 2009). **B.** Comparison of extant and fossil arvicoline (voles and lemmings) and murine (IC model) molar proportions in the Kavanagh prediction model. We observe decreasing inhibition between the majority of arvicolines (m1 > > m2 = m3) and the other individuals (lemmings, m1 > m2 = m3). True lemming and vole morphospaces are delimited by perpendicular gray lines. Tooth drawings illustrate different molar proportions, with their corresponding symbol circled. m1 > > m2 = m3, m1 > m2 < m3, m1 > m2 > m3, and m1 > m2 = m3 represent *Microtus agrestis*, *Lagurus lagurus*, *Clethrionomys glareolus*, and *Lemmus lemmus*, respectively (from Renvoisé et al., 2009).

Fig. 4. Vue occlusale des molaires inférieures (de m1 à m3) de *Microtus arvalis*, et représentation de la modularité (rectangles noirs). Les processus développementaux responsables de la modularité sont symbolisés par des flèches, dont l'épaisseur indique le degré d'intégration, et dont le type de trait (continu ou tireté) symbolise deux processus différents (d'après Laffont et al., 2009). **B.** Comparaison des proportions de molaires d'arvicolinés actuels et fossiles (campagnols et lemmings) et de murinés (IC model) dans le modèle prédictif de Kavanagh. On observe une baisse d'inhibition entre la plupart des arvicolinés (m1 > > m2 = m3) et les autres individus (lemmings, m1 > m2 = m3). Les espaces morphologiques des vrais lemmings et des campagnols sont délimités par des lignes grises perpendiculaires. Des dessins dentaires illustrent différentes proportions de molaires, avec leur symbole en cercle correspondant. m1 > > m2 = m3, m1 > m2 < m3, m1 > m2 > m3, et m1 > m2 = m3 représentent respectivement *Microtus agrestis*, *Lagurus lagurus*, *Clethrionomys glareolus*, and *Lemmus lemmus*, respectivement (d'après Renvoisé et al., 2009).

genetic properties of organisms and on the magnitude of environmental stresses occurring during development. Morphometric methods used to detect asymmetries are either based on linear distances, or on landmark data (for a discussion on the possible biases of fluctuating asymmetry detection, see Stige et al. (2006)). We sum up below the main results of four works to exemplify the relevance of asymmetry studies (for further applications of asymmetry studies on morphological data see Debat et al. (2000); Garnier et al. (2006)).

The impact of anthropization of environment was assessed in voles (Marchand et al., 2003) and in sea urchins (Saucède et al., 2006). In the former work (Marchand et al., 2003), four populations of bank voles (*Clethrionomys glareolus*) were sampled near the Mont-St-Michel Bay (France). Three of them were characteristic of fragmented and intensively farmed landscapes, supposed to decrease genetic diversity in populations and to increase stress during individual development. Another population came from a less anthropized area (hedged farmland). Measures of fluctuating asymmetry on skulls and teeth confirmed this hypothesis of stress, as populations from intensively farmed areas exhibited a higher degree of fluctuating asymmetry than the population from the less disturbed area. In (Saucède et al., 2006), two populations of the sea urchin *Echinocardium flavescens* from Norwegian coasts

were studied. One of the two populations was marked by a polluted environment. Fluctuating asymmetry levels were mainly quantified from plates from the ambulacra. The highest levels of fluctuating asymmetry were exhibited by the population living in the most stressing habitat. An originality of this work is the use of bilateral symmetry to detect asymmetries, rather the more intuitive pentaradial symmetry for echinoderms. This choice is discussed in the light of knowledge about urchin development.

Environmental stresses affecting organism development can also be of biological origin. Indeed, in Alibert et al. (2002), the effect of the presence of two acanthocephalan parasite species (*Pomphorhynchus laevis* and *P. minutus*) on the development of their intermediate host (the gammarid *Gammarus pulex*) was assessed. The main results are: (i) higher levels of fluctuating asymmetry in infected individuals, suggesting that the infection could act as a significant stress affecting gammarids during their development; and (ii) higher level of fluctuating asymmetry in males than in females, discussed in terms of sexual selection.

Finally, the genetic basis of developmental instability has also been considered through a review of the literature focusing on the relationship between fluctuating asymmetry and hybrid dysgenesis (Alibert and Auffray, 2003). This survey has confirmed the prominent role that genomic coadaptation can play in developmental

stability and therefore the interest of such morphological approaches for the study of population differentiation and speciation. However, it also points out that predictions remain difficult to make, because the outcome depends on several factors such as the type of genomic interactions acting in hybrids or the nature of traits studied.

3.2. Developmental modularity and prediction model for the evolution of vole molars

Modularity is defined by the fact that organisms are divided into biological parts which are hierarchically structured and partially integrated to ensure coherence, and these parts evolve more or less independently from the rest of organisms (Bolker, 2000; Cheverud, 1996; Wagner, 1996). Whereas most modularity and integration studies on mammals have dealt with skulls (e.g. Cheverud, 1995; Drake and Klingenberg, 2010; Goswami, 2006; Hallgrímsson et al., 2004; Marroig and Cheverud, 2001; Mitteroecker and Bookstein, 2008) and mandibles (e.g. Klingenberg et al., 2003; Márquez, 2008; Monteiro et al., 2005; Zelditch et al., 2009), a recent study focused on teeth, and particularly on the vole lower molar row (Laffont et al., 2009). The characterization of the degree of developmental integration/modularity of sets of morphological traits can be performed by studying patterns of covariation within and among individuals from landmark data (Klingenberg, 2009). This method also assesses the developmental causes of integration/modularity patterns (Fig. 4A). By applying this approach to vole molars (Laffont et al., 2009), results have suggested: (i) quasi-independence of each molar shape at the developmental level (developmental modules), even slightly stronger for the third molar, as demonstrated by genetic and developmental hypotheses; and (ii) more pervasive integration processes among molars at the morphological level.

Additionally, a model established from murine dental development (Kavanagh et al., 2007) has recently been proposed to predict evolutionary patterns in lower murine teeth and has been extrapolated in extant and fossil mammalian species (Polly, 2007). Changes in inhibitor or activator produce modifications in molar tooth proportions and lead to different morphotypes. However, some taxa do not fit the model (Polly, 2007), such as voles, due to their oversized first lower molar. In a recent work (Renvoisé et al., 2009), the scope of the macroevolutionary model was broadened by projecting a time scale on to the developmental model (as suggested by Raff, 2007), including extant, fossil and extinct species of voles but also of other rodent families (Fig. 4B). It was demonstrated that arvicoline (i.e. voles and lemmings) evolution is rather marked by a large gap from the oldest to more recent genera with a rapid acquisition of a large first lower molar contemporaneous to their radiation. A new model was described that can characterize nonlinear molar proportions in mammals. This work underlined the necessity of adding fossil data to evolutionary developmental studies to highlight macro-evolutionary trajectories through time.

4. Conclusion

In the paper by Neige et al. (1997), case studies showed an overview of morphometric studies in our laboratory at the end of the 1990 s. Morphometrics was mainly used to understand how past and present disparity is structured, by comparing morphometric data to temporal (via stratigraphy), ecological or ontogenetic data. Through the few examples presented above, it appears that disparity and its evolution are still key issues in morphometric studies. Nevertheless, advancements in morphometrics, for example, with the development of tools inferring developmental stability or modularity from shapes, enable to processes responsible for disparity to be assessed. Finally, it is worthwhile mentioning that the efficiency of morphometric tools is not only acknowledged in evolutionary biology, but also in other fields that are starting (or have started) using them. For instance, in biomechanics, motion analyses can be processed by the monitoring of landmarks through time on the same structure (e.g. Adams and Cerney, 2007; Decker et al., 2007); in statistics, matrix comparisons can be made using Procrustes fitting methods rather than the more traditional Mantel test (Peres-Neto and Jackson, 2001). It is likely that the morphometric revolution is just starting.

Acknowledgements

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