

BIOLOGY SERIES



Systematics and the Exploration of Life

**Edited by
Philippe Grandcolas
Marie-Christine Maurel**

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Systematics and the Exploration of Life

Series Editor
Marie-Christine Maurel

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111 River Street
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Library of Congress Control Number: 2020949898

British Library Cataloguing-in-Publication Data
A CIP record for this book is available from the British Library
ISBN 978-1-78630-265-6

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Introduction

Exploring Biodiversity: Science Must Seize the Unknown 80%

We actually know far too little about biodiversity! We are idly living on the improved achievements of a period of intense exploration, which lasted from the 18th century through to the beginning of the 20th century, with the beginnings of “systematics”.

The modern formalized description of the diversity of life was born at the beginning of this period, namely the famous *Systema Naturae* by Carl Linnaeus (1758). These first classifications were constructed on the basis of an implicit order in life, as perceived by precursor authors. This comparative perception and the linking of structures between different organisms are, indeed, at the heart of the origin of the theory of evolution (Le Guyader 2018; Montévil 2019).

While the progress of systematics waned at the beginning of the 20th century, general biology developed extraordinarily. It focused on the study of the laws of life through the study of a few organisms that imposed themselves as “models”, from the vinegar fly to the white rat. Immense discoveries were made about heredity, the functioning of organisms and living cells, which today form the basis of our general knowledge (Mayr 1982). In comparison, the exploratory and still descriptive approach to the diversity of living organisms was gradually becoming obsolete; it suffered from enunciating particulars rather than the universals of general biology (Mahner and Bunge 1997; Grandcolas 2017).

Fortunately, the subsequent development of a comparative methodology and phylogenetic analysis revived this field and enabled it to make a strong contribution to modern evolutionary biology (Nelson 1970). Biology then rediscovered the diversity of organisms (Wilson 1988), making a new synthesis by considering the general laws of life *and* the diversity of their expression in living organisms (Grandcolas 2018).

The balance sheet of these past decades of exploration is both extraordinary, commensurate with biological diversity and these glorious periods of discovery *ab nihilo*, and disappointing, as we too often capitalize on a false feeling of déjà vu (Grandcolas 2017).

And yet, to give just one figure, we currently only know about two million living species, in other words, less than 20% of the 10 million species whose existence has been statistically inferred on numerous occasions (May 1988). Study after study on the many groups of organisms shows how much remains to be discovered, whether small or large, or near or far from us (e.g. Bouchet 2006; Vieites *et al.* 2009; De Vargas *et al.* 2015; Hawksworth and Lücking 2017; Nicolas *et al.* 2017). We still know very little about most of the so-called “species known to science”. We only have a few lines in old publications which describe more than half of the macro-organisms (Troudet *et al.* 2017) and a few molecules, instead of whole phenotypes on uncultured microbes (Konstantinidis *et al.* 2017).

The issue now is to understand that it is essential to discover the unknown 80% of biodiversity for several well-defined scientific reasons, more than for the thirst for new knowledge or for a compulsive collection of new species.

First of all, the laws of life have rather varied degrees of generality; from heredity to the functioning of ecosystems, for example, there are several orders of magnitude of difference in this respect! Many laws or principles require the study of more particulars in order to reach generality, given the variation that is the intrinsic property of living things (Montévil *et al.* 2016). Clearly, we need to know about more organisms and the particular cases of their biology in order to be able to claim to generalize. The rules of representativeness, dominance or abundance, stated as truisms, are often misleading in living organisms. For example, it has recently been documented that rare and scarce species often fulfill disproportionately important functional roles within ecosystems (Mouillot *et al.* 2013).

In contrast to universals, particulars very frequently remind us of how many pathogenic, invasive species are discovered in this way, having already crossed half the planet, causing us great concern. This is as much the case for HIV (Barré-Sinoussi *et al.* 1983), an obscure retrovirus from an African primate, as for an invasive and unknown flatworm imported from South America, threatening the fauna of our soils and their faunal balance (Justine *et al.* 2020). Not a week goes by without a species new to science presenting a question to our societies. The COVID-19 pandemic is a dramatic demonstration of this: here again, a few poorly known bats and pangolins harbor unknown (and described for the occasion) coronaviruses whose genetic recombination is putting the human world at a standstill (Hassanin *et al.* 2020). This is also the case for viruses and viroids of plants that are still largely unknown, and vectors of devastation in some plantations (Maurel 2018).

The issue of bio-inspiration (Benuys 1997) is another opportunity to understand how much the diversity of living things contains wonders from which we can draw inspiration for more sustainable societies; so many particulars (structures, functions, etc.) in different species whose natural function can be transposed to functions of human interest. Practicing bio-inspiration beyond random discoveries of opportunity requires a broad and reasoned exploration of living things and the relationships between their structures and functions.

Particulars are also often geographical rather than purely taxonomic. Each state, government or municipality needs to be aware of local biodiversity in order to develop a reserve or environmental, agricultural or health policies (Pellens and Grandcolas 2016). These are all reasons to be aware of local fauna and flora with their innumerable numbers of endemic species (Caesar *et al.* 2017). It is worth remembering the order of magnitude of these numbers and that there are, for example, 40,000 species of insects in metropolitan France alone (Gargominy *et al.* 2014).

Even if we focus on a few species for reasons of immediate interest, it is essential to know their close relatives. Knowing the meaning, adaptive character and selection regime of the traits of organisms, whether they are genotypic or phenotypic models, requires an understanding of their history (Jenner 2006). Is it necessary, once again, to quote Dobzhansky (1973) – “nothing in biology makes sense except in the light of evolution” – to be convinced of this. Reconstructing the origin and evolution of the traits of an

organism of interest requires knowing not only its close relatives, but also a very large part of the living world. How many fundamental traits has the human species inherited, the understanding of which is based on their structure and function at the Metazoan scale (more than a million species!)? This presupposes an adequate taxonomic sampling of life, which is not necessarily limited to known species, but which must be searched for out in the field in order to find unknown species whose lifestyles have sometimes been long surmised.

The entirety of this book is therefore dedicated to these approaches to exploring the diversity of life, each of them showing the crucial need we have for exploratory approaches. “Exploratory”, which is easy to understand when reading this volume, does not refer to a kilometric description of specific characteristics, but to an organization of knowledge and hypothesis tests, based on a large sampling of living species – a large part of which is, strangely, still unknown to us, even though we come into contact with it every day. Without further delay, we must not suffer from or destroy biodiversity, but study it in order to integrate it sustainably into our societies.

References

- Barré-Sinoussi, F., Chermann, J.C., Rey, F., Nugeyre, M.T., Chamaret, S., Gruest, J., Dauguet, C., Axler-Blin, C., Vezinet-Brun, F., Rouzioux, C., Rozenbaum, W., and Montagnier, L. (1983). Isolation of a T-lymphotropic retrovirus from a patient at risk for acquired immune deficiency syndrome (AIDS). *Science*, 220, 868–871.
- Benyus, J.M. (1997). *Biomimicry: Innovation Inspired by Nature*. Harper Perennial, New York.
- Bouchet, P. (2006). The magnitude of marine biodiversity. In *The Exploration of Marine Biodiversity: Scientific and Technological Challenges*, Duarte, C.M. (ed.). Fundacion BBVA, Bilbao, Spain, 31–62.
- Caesar, M., Grandcolas, P., and Pellens, R. (2017). Outstanding micro-endemism in New Caledonia: More than one out of ten animal species have a very restricted distribution range. *PLOS One*, 12(7), e0181437.
- Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher*, 35, 125–129.
- Gargominy, O., Tercerie, S., Régnier, C., Ramage, T., Schoelinck, C., Dupont, P., and Poncet, L. (2014). TAXREF v8.0, référentiel taxonomique pour la France : méthodologie, mise en œuvre et diffusion. SPN report, 42.

- Grandcolas, P. (2017). Loosing the connection between the observation and the specimen: A by-product of the digital era or a trend inherited from general biology? *Bionomina*, 12, 57–62.
- Grandcolas, P. (2018). The view of systematics on biodiversity. In *Biodiversity and Evolution*, Grandcolas, P. and Maurel, M.-C. (eds). ISTE Ltd, London and John Wiley & Sons, New York, 29–38.
- Hassanin A., Grandcolas P. & Veron G. (2020). Covid-19: Natural or anthropic origin? *Mammalia*, 000010151520200044.
- Hawksworth D.L. and Lücking R. (2017). Fungal Diversity Revisited: 2.2 to 3.8 Million Species. In *The Fungal Kingdom*, Heitman J, Howlett BJ, Crous PW, Stukenbrock EH, James TY and Gow NAR (eds). American Society for Microbiology, Washington, DC, 79–95.
- Jenner, R.A. (2006). Unburdening evo-devo: Ancestral attractions, model organisms, and basal baloney. *Development Genes and Evolution*, 216, 385–394.
- Justine, J.L., Winsor, L., Gey, D., Gros, P., and Thévenot, J. (2020). *Obama chez moi!* The invasion of metropolitan France by the land planarian *Obama nungara* (Platyhelminthes, Geoplanidae). *PeerJ*, 8, e8385.
- Konstantinidis, K.T., Rosselló-Móra, R., and Amann, R. (2017). Uncultivated microbes in need of their own taxonomy. *The ISME Journal*, 11, 2399–2406.
- Le Guyader, H. (2018). *Classification et évolution*. Le Pommier, Paris.
- Linnaeus, C. (1758). *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, 10th edition, volume 1. Laurentii Salvii, Holmiae, Stockholm.
- Mahner, M. and Bunge, M. (1997). *Foundations of Biophilosophy*. Springer, Berlin.
- Maurel, M.-C. (2018). À la frontière du vivant: les viroïdes [Online]. *The Conversation*. Available: <https://theconversation.com/a-la-frontiere-du-vivant-les-viro-des-90500>.
- May, R.M. (1988). How many species are there on earth? *Science*, 241(4872), 1441–1449.
- Mayr, E. (1982). *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Harvard University Press, Cambridge.
- Montévil, M. (2019). Measurement in biology is methodized by theory. *Biology & Philosophy*, 34(3), 35.
- Montévil, M., Mossio, M., Pocheville, A., and Longo, G. (2016). Theoretical principles for biology: Variation. *Progress in Biophysics and Molecular Biology*, 122, 36–50.

- Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J., and Thuiller, W. (2013). Rare species support vulnerable functions in high-diversity ecosystems. *PLOS Biology*, 11, e1001569.
- Nicolas, V., Martínez-Vargas, J., and Hugot, J.P. (2017). *Talpa aquitania* sp. nov. (Talpidae, Soricomorpha), a new mole species from SW France and N Spain. *Mammalia*, 81(6), 641–642.
- Pellens, R. and Grandcolas, P. (eds) (2016). *Biodiversity Conservation and Phylogenetic Systematics: Preserving Our Evolutionary Heritage in An Extinction Crisis*. Springer International Publishing, New York.
- TrouDET, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., and Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, 7, 9132.
- de Vargas C., Audic S., Henry N. *et al.* (2015). Eukaryotic plankton diversity in the sunlit ocean. *Science*, 348, 1261605.
- Vieites, D.R., Wollenberg, K.C., Andreone, F., Kohler, J., Glaw, F., and Vences, M. (2009). Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences of the USA*, 106, 8267–8272.
- Wilson, E.O. (ed.) (1988). *Biodiversity*. National Academies Press, Washington.

Symmetry of Shapes in Biology: from D'Arcy Thompson to Morphometrics

1.1. Introduction

Any attentive observer of the morphological diversity of the living world quickly becomes convinced of the omnipresence of its multiple symmetries. From unicellular to multicellular organisms, most organic forms present an anatomical or morphological organization that often reflects, with remarkable precision, the expression of geometric principles of symmetry. The bilateral symmetry of lepidopteran wings, the rotational symmetry of starfish and flower corollas, the spiral symmetry of nautilus shells and goat horns, and the translational symmetry of myriapod segments are all eloquent examples (Figure 1.1).

Although the harmony that emanates from the symmetry of organic forms has inspired many artists, it has also fascinated generations of biologists wondering about the regulatory principles governing the development of these forms. This is the case for D'Arcy Thompson (1860–1948), for whom the organic expression of symmetries supported his vision of the role of physical forces and mathematical principles in the processes of morphogenesis and growth. D'Arcy Thompson's work also foreshadowed the emergence of a science of forms (Gould 1971), one facet of which is a new branch of biometrics, morphometrics, which focuses on the quantitative description of shapes and the statistical analysis of their variations. Over the past two decades, morphometrics has developed a methodological

Chapter written by Sylvain GERBER and Yoland SAVRIAMA.

framework for the analysis of symmetry. The study of symmetry is today at the heart of several research programs as an object of study in its own right, or as a property allowing developmental or evolutionary inferences. This chapter describes the morphometric characterization of symmetry and illustrates its applications in biology.

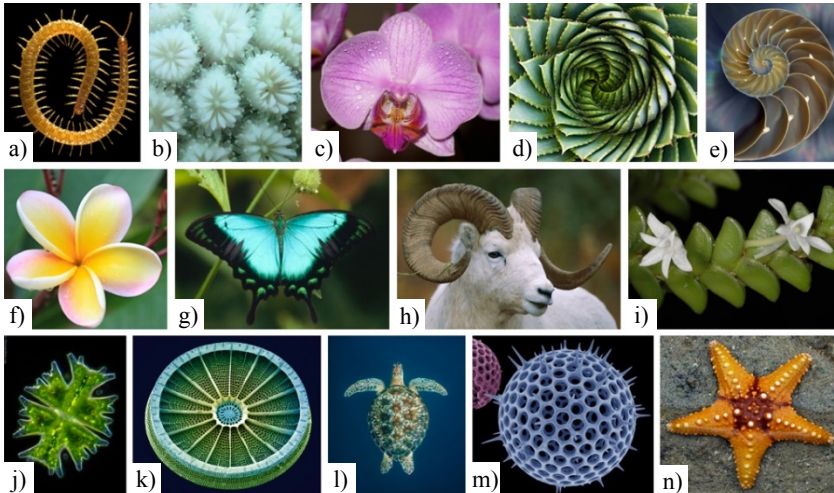


Figure 1.1. Diversity of symmetric patterns in the living world. For a color version of this figure, see www.iste.co.uk/grandcolas/systematics.zip

COMMENTARY ON FIGURE 1.1. – a) Centipede (*C. Brena*); b) corals (*D. Caron*); c) orchid (*flowerweb*); d) spiral aloe (*J. Cripps*); e) nautilus (*CC BY 3.0*); f) plumeria (*D. Finney*); g) Ulysses butterfly (*K. Wothe/Minden Pictures*); h) capri (*P. Robles/Minden Pictures*); i) *Angraecum distichum* (*E. hunt*); j) *desmidiale* (*W. Van Egmond*); k) diatom (*S. Gschmeissner*); l) sea turtle (*T. Shultz*); m) radiolarian (*CC BY 3.0*); n) starfish (*P. Shaffner*).

1.2. D’Arcy Thompson, symmetry and morphometrics

A century has passed since the original publication of D’Arcy Thompson’s major work, *On Growth and Form* (1917). On the occasion of this centenary, several articles have celebrated his magnum opus, highlighting the originality and enduring influence of some of Thompson’s ideas in disciplines such as mathematical biology, physical biology, developmental biology and morphometrics (see Briscoe and Kicheva (2017),

Keller (2018) and Mardia *et al.* (2018) for specific reviews of these various contributions).

Thompson's main thesis is that "physical forces", such as gravity or surface tension phenomena, play a preponderant role in the determinism of organic forms and their diversity within the living world. His structuralist conception of the diversity of forms is accompanied by a critique of the Darwinian theory of evolution, but this critique is in fact based on an erroneous interpretation of the causal context (efficient cause vs. formal cause) presiding over the emergence of forms (Medawar 1962; Gould 1971, 2002, p. 1207).

The notion of symmetry is present in the backdrop throughout the book. The successive chapters go through the different orders of magnitude of the organization of life and the physical forces that prevail at each of these scales. The skeletons of radiolarians, the spiral growth of mollusk shells and the diversity of phyllotactic modes are some of the examples illustrating the pivotal role of symmetry in the architecture of biological forms. This interest in symmetry is in line with the work of Ernst Haeckel, whose book *Kunstformen der Natur* (Haeckel 1899) offers bold anatomical representations emphasizing (and sometimes idealizing) the exuberance and sophistication of symmetry patterns found in nature. Thompson sees the harmony and regularity of symmetric forms as the geometric manifestation of the mathematical principles that establish a fundamental basis for his theory of forms.

This emphasis on geometry finds its clearest expression in the last and most famous chapter of the book, "On the theory of transformation, or the comparison of related forms" (Arthur 2006). Thompson proposes a method for comparing the forms between related taxa, based on the idea of (geometric) transformation from one form to another, by means of continuous deformations of varying degrees of complexity. The morphological differences (location and magnitude) are then graphically expressed by applying the same transformation to a Cartesian grid placed on the original form. In spite of his admiration for mathematics, Thompson's approach nevertheless remains qualitative and without a formal mathematical framework for its empirical implementation. These graphical representations will, however, have a considerable conceptual impact on biologists working on the issues of shape and shape change. Several more or less elegant and operational attempts at quantitative implementation were made during the 20th century (see Medawar (1944), Sneath (1967) and Bookstein (1978), for example), up until the formulation of deformation grids using the

thin-plate splines technique proposed by Bookstein (1989), which is still in use today.

Beyond the questions of symmetry, Thompson's idea of combining geometry and biology to study shapes remains at the heart of the principles and methods of modern morphometrics (Bookstein 1991, 1996).

1.3. Isometries and symmetry groups

In this section, we propose an overview of the mathematical characterization of the notion of symmetry, as it can be applied to organic forms. The physical environment in which living organisms evolve is comparable to a three-dimensional Euclidean space. It is denoted by \mathbf{E}^3 . A geometric figure is said to be *symmetric* if there are one or more transformations which, when applied to the figure, leave it unchanged. Symmetry is thus a property of invariance to certain types of transformations. These transformations are called *isometries*.

Formally, an isometry of the Euclidean space \mathbf{E}^3 is a transformation $T: \mathbf{E}^3 \rightarrow \mathbf{E}^3$ that preserves the Euclidean metric, that is, a transformation that preserves lengths (Coxeter 1969; Rees 2000):

$$d(T(x), T(y)) = d(x, y)$$

for all x and y points belonging to \mathbf{E}^3 .

The different isometries of \mathbf{E}^3 are obtained by combining rotation and translation ($x \mapsto Rx + t$, where R is an orthogonal matrix of order 3 and t is a vector of \mathbb{R}^3). They include the identity, translations, rotations around an axis, screw rotations (rotation around an axis + translation along the same axis), reflections with respect to a plane, glide reflections (reflection with respect to a plane + translation parallel to the same plane) and rotatory reflections (rotation around an axis + reflection with respect to a plane perpendicular to the axis of rotation). The set of isometries for which an object is invariant constitutes the *symmetry group* of the object.

For biologists wishing to explore symmetry in an organism, the correct identification of the symmetry group is important because it conditions the relevance of the morphometric analysis to come. The symmetry group of the

organic form is always a subgroup of the isometries of \mathbf{E}^3 . In particular, the translation has no exact equivalent in biology, since the physical extension of an organism is finite (the finite repetition of arthropod segments, for example). Translational symmetry is therefore approximate. The other isometries form a finite subgroup of Euclidean isometries, including the cyclic and dihedral groups, as well as the tetrahedral, octahedral and icosahedral groups of the Platonic solids that were dear to Thompson (1942, Chapter 9). It appears that, essentially, the symmetry patterns of biological shapes correspond to cyclic groups (rotational symmetry of order n alone [C_n], or combined with a plane of symmetry perpendicular to the axis of rotation [C_{nh}], or with n planes of symmetry passing through the axis of rotation [C_{nv}]). The bilateral symmetry of bilaterians corresponds, for example, to the group C_{1v} , in other words, a rotation of $2\pi/1$ (identity) combined with a reflection across a plane passing through the rotation axis.

1.4. Biological asymmetries

Another aspect of the imperfect nature of biological symmetry rests on the existence of deviations from the symmetric expectation (Ludwig 1932). These deviations manifest themselves to varying degrees and have distinct developmental causes. Let us consider the general case of a biological structure, whose symmetry emerges from the coherent spatial repetition of a finite number of units (e.g. the two wings of the drosophila, the five arms of the starfish). Different types of asymmetry are recognized (see also Graham *et al.* (1993) and Palmer (1996, 2004)):

- *directional asymmetry* corresponds to the case where one of the units tends to systematically differ from the others in terms of size or shape. A classic example is the narwhal, whose “horn” is in fact the enlarged canine tooth of the left maxilla, while the vestigial right canine tooth remains embedded in the gum;

- *antisymmetry* is comparable in magnitude to directional asymmetry, but the unit that differs from the others in size or shape is not the same from one individual to another. The claws of the fiddler crab show this type of asymmetry, the most developed claw being the right or the left, depending on the individual;

- *fluctuating asymmetry* is an asymmetry of very small magnitude and is therefore much more difficult to detect. It is the result of random inaccuracies in the developmental processes during the formation of the

units that compose the biological structure. Fluctuating asymmetry is *a priori* always present, even if it is not always measurable. Its magnitude is considered a measure of developmental precision and has often been used (albeit sometimes controversially) as a marker of stress.

Geometrically, the morphological variation in a sample of biological shapes exhibiting a symmetric arrangement can thus be decomposed into symmetric and asymmetric variations. There is only one way to be perfectly symmetric with respect to the symmetry group of the considered structure (this is the case when all the isometries of the group are respected), but there are one less many ways to deviate from perfect symmetry as there are isometries in the group. Thus, the total variation always includes one symmetric component and at least one asymmetric component. Geometric morphometrics offers mathematical and statistical tools to quantify and explore this empirical variation.

1.5. Principles of geometric morphometrics

We are limiting ourselves here to the morphometric framework, in which the morphology of a biological structure is described by a configuration of p landmarks (Bookstein 1991; Rohlf and Marcus 1993; Adams *et al.* 2004). These landmarks, ideally defined on anatomical criteria, must be recognizable on all n specimens of the sample. Their digitization in $k = 2$ or 3 dimensions (depending on the geometry of the object considered) provides a description of each specimen as a series of pk coordinates. The comparison of the two or more objects thus characterized is done by superimposing their landmark configurations. The method most commonly used today is the Procrustes superimposition (Dryden and Mardia 1998). The underlying idea is that the shape of an object can be formally defined as the geometric information that persists once it is freed from differences in scale, position and orientation (Kendall 1984). These non-informative differences in relation to the shape are eliminated by scaling, translation and rotation, so as to minimize the sum of the squared distances between homologous landmarks (Figure 1.2). The residual variation provides a measure of the shape difference between the two objects, the *Procrustes distance*, which constitutes the metric of the *shape space*. In this space, each point corresponds to a shape, and two shapes are all the more similar, the smaller the Procrustes distance is between the points that represent them.

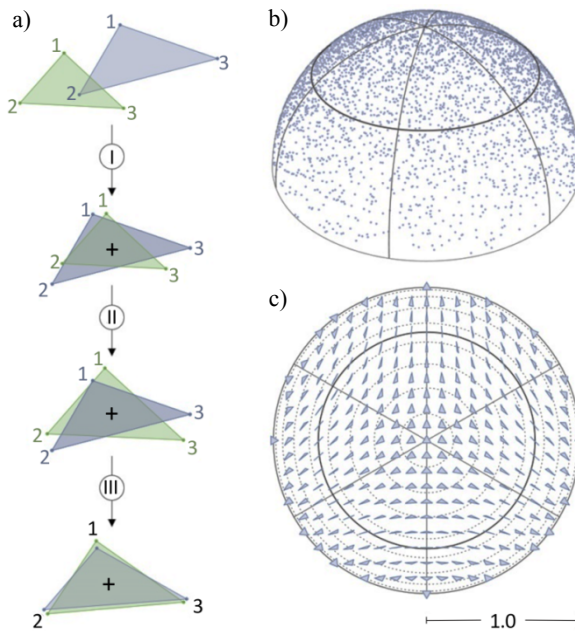


Figure 1.2. Principles of geometric morphometrics illustrated for the simple case of triangles (three landmarks in two dimensions). For a color version of this figure, see www.iste.co.uk/grandcolas/systematics.zip

COMMENT ON FIGURE 1.2. – a) Two objects described by homologous configurations of landmarks are subjected to three successive transformations eliminating the differences in position (I), scale (II) and orientation (III), in order to extract a measure of their shape difference: the Procrustes distance. b) The Procrustes distance is the metric of the shape space, a non-Euclidean space in which each point corresponds to a unique shape. In applied morphometrics, researchers work with a space related to the shape space called the Procrustes (hyper)hemisphere. c) The non-linearity of this space requires projecting data onto a tangent space before testing biological hypotheses by using traditional statistical methods.

Empirical applications of morphometrics are generally carried out in another space, the Procrustes (hyper)hemisphere, mathematically linked to the shape space, and efficiently estimating distances between shapes when the studied morphological variation is small compared to the possible