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Comparative morphology at a crossroads

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Abstract

Morphology has been the fundamental and most important source of information in biology. We strongly believe that in the current molecular era of biology, comparative morphology still has an important role to play in understanding life on Earth and ecosystem functioning, bridging the knowledge gap between evolution, systematics, and ecology.

KEYWORDS

evolution, funding, phylogenetics, systematics, training, Tree of Life

THE CHANGING ROLE OF COMPARATIVE MORPHOLOGY

Since the earliest attempts to classify life on Earth, comparative morphology (Box 1) has been the primary source of information for describing and classifying species (Jeiter and Smets, 2023). In the 19th and 20th centuries, morphology was supplemented by a plethora of other sources of information to classify organisms, such as palynology, palaeontology, biogeography, and chemotaxonomy. The emergence of DNA-based molecular phylogenetics in the 1990s brought another new wave of methods and theoretical approaches to systematics. The rapid rise of DNA sequencing coupled with powerful tree-building algorithms has enabled us to gain a deep understanding of the evolution of life on Earth; see for example the DToL-project (Darwin Tree of Life Project Consortium et al., 2022), the APG-system (APG IV, 2016), and the PAFTOL-Project (Zuntini et al., 2024).

We agree with Wanntorp and Ronse De Craene (2011) that these classification systems, based on molecular phylogenetics, provide excellent opportunities to study the evolution of morphological traits. Many questions remain about the forms, functions, and ecological roles of most traits, as well as the underlying evolution leading to the observed diversity. Phylogenetic trees themselves provide insights into the evolutionary relationships of organisms, but we also need to understand the developmental processes that shape the characters that make up the Tree of Life. Data sets of morphological traits are used to understand the evolution of life on Earth. For example, Sauquet et al. (2017) conducted a study that offered new insights into the morphology of the ancestral flower of angiosperms, which sheds light on the origin of flower diversity and the overall angiosperm evolution. Although the approach of Sauquet et al. (2017) yields interesting results, the gaps in our understanding of the morphological traits considered and their presumed homologies, caused by the lack of developmental information, may lead to far-reaching conclusions that could lead to incorrect interpretations of evolution. Another example of the potential value of comparative morphology is its use in understanding the origins of insular woodiness—the evolutionary transition from herbaceous plants into woody species on islands—and drought stress-related traits

Julius Jeiter and Erik Smets contributed equally.

BOX 1 Defining comparative morphology and development.

Morphology is the study of the form of organisms or their parts. It is necessary to understand the function of structures and to classify organisms. Comparative morphology does the same, but its main aim is to compare the form of organisms or their parts to understand their evolution. In general, it is the external form that is studied in morphology, whereas the internal structure is the subject of anatomy or histology. For the sake of simplicity, we will use morphology in its broadest sense, including anatomy and histology. Organisms are dynamic and constantly developing throughout their lives. Understanding how they develop is a crucial aspect of comparative morphology (Figure 1; Jeiter and Smets, 2023).

(Zizka et al., 2022). This understanding will help in taking measures to combat the impacts of climate change (UN General Assembly, 2015), for instance, through crop improvement or predicting future adaptations. Morphology has also inspired applications in the field of biomechanics, for example, a hingeless flapping mechanism based on observations of the pollination mechanism of *Strelitzia reginae* flowers (Lienhard et al., 2011).

COMPARATIVE MORPHOLOGY'S SIGNIFICANCE AND EFFECTS

Morphologically (often superficially) similar structures that have evolved in response to similar environmental and/or physiological pressures in unrelated groups (i.e., convergent evolution) are a great example of an active area of research in morphology. Understanding morphological structures through developmental stages is necessary to assess whether such structures are truly homologous (i.e., share a common evolutionary origin and developmental pathway; Figure 1; Ochoterena et al., 2019).

Comparative morphology also contributes to the field of evolutionary developmental genetics (i.e., EvoDevo), which aims to understand the genetic mechanisms underlying development. EvoDevo studies require expertise in both genetics and comparative morphology to correctly interpret the results of developmental studies, as highlighted by the coining of the term MorphoEvoDevo (Wanninger, 2015; Petrone-Mendoza et al., 2023). In the early days, many EvoDevo studies focused heavily on a few model organisms such as *Arabidopsis thaliana* and *Oryza sativa*. Later, studies on a wide range of organisms strengthened the field. As flower morphologists, we are naturally drawn to examples that contribute to our understanding of how genes determine the morphological traits of angiosperms. Cullen et al. (2023) identified genes that are expressed during spur development in *Linaria vulgaris*. These may be candidates for the development of other tubular projections in flowering species and may lead to an understanding of the evolution of spurs. Organ fusion within the same or different whorls, forming complex structures, has occurred multiple times independently in angiosperm evolution, suggesting a conserved underlying regulatory network. Phillips et al. (2020) reviewed the developmental basis of different fusion phenotypes and the role of the reduced expression of *NAM/CUC3* (*NO APICAL MERISTEM/CUP-SHAPED COTYLEDON*) genes leading to the independent evolution of fused organs. Further research on these genes could elucidate the fusion processes and their significance in angiosperm evolution. Although these types of studies are important, they highlight the need for more comparative morphological observations to identify all the phenotypes and their development.

Ultimately, a deeper morphological understanding of the branches of the Tree of Life is needed to build a predictive classification system that allows us to anticipate the occurrence of certain traits or the position of taxa (Dahlgren, 1980). In-depth studies of morphology in the context of evolution using modern methods such as Micro-Computed Tomography (μCT), Light-Sheet Microscopy, Magnetic Resonance Imaging, and Geometric Morphometrics (Ledford, 2018; Borisjuk et al., 2023) open new possibilities for understanding evolution; an example from our own research include a study of specialized floral structures related to bee pollination in orchids using μCT and EvoDevo (Pramanik et al., 2020).

THE URGENCY OF COMPARATIVE MORPHOLOGY

Despite the availability of molecular phylogenies, and increasingly sophisticated methods for studying and visualizing morphology, development, and the underlying gene expressions (Ledford, 2018), there is a risk that the skills needed to acquire and interpret comparative morphological data are being lost. Comparative morphology links molecular phylogenetics with ecology enabling us to fully understand the intimate relationships among plants and animals, which are beautifully portrayed in captivating wildlife documentaries and natural history museums. It provides insights into both evolution and function, bridging the gap between systematics and applied sciences (Strelin et al., 2023). Even for supposedly well-known species and taxa, our knowledge of their morphology remains incomplete (Wanntorp and Ronse De Craene, 2011). This has serious implications for various disciplines such as biomechanics, biomimetics, plant breeding, and phenotyping and developmental genetics. All these disciplines rely on accurate morphological descriptions.

We argue that the power of morphology should not be neglected in current systematic, EvoDevo, and evolutionary research. Such an integrated approach to morphology, taxonomy, and molecular systematics will lead to a better understanding of evolutionary relationships, which in turn will lead to a better assessment of ecosystem functioning and a further

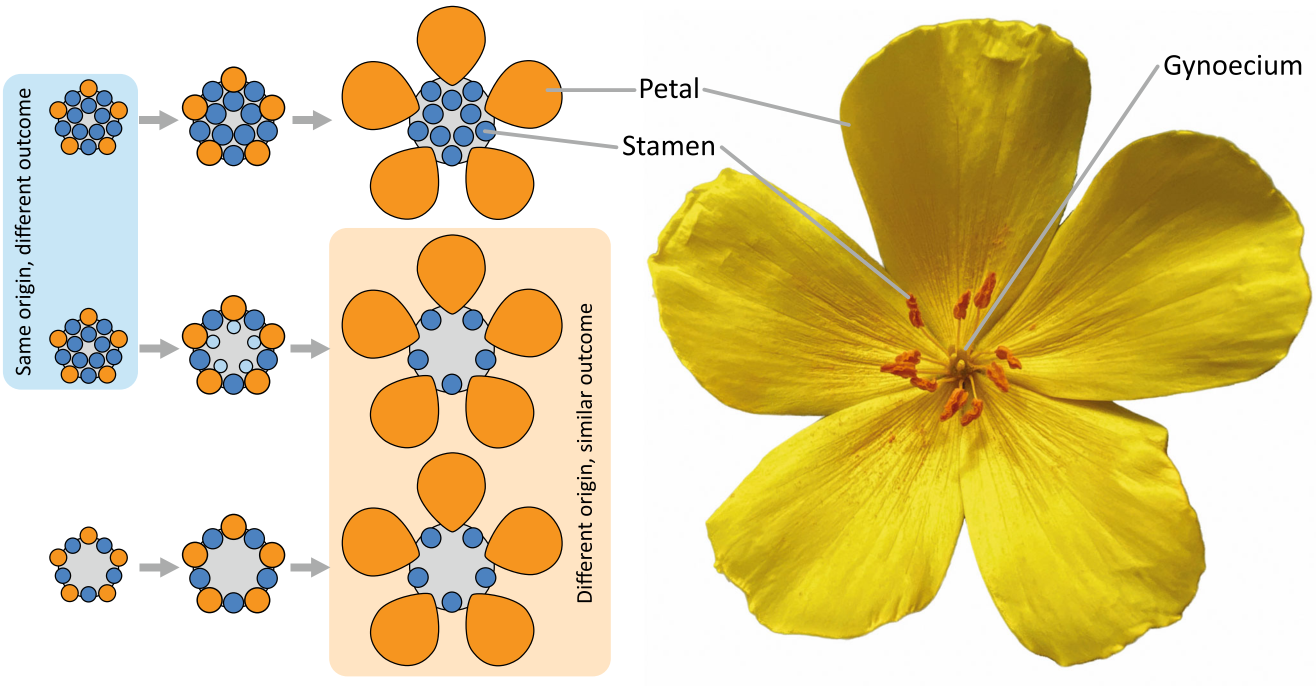

FIGURE 1 Illustration of the relationship between the early developmental stage and the mature state of flowers. Orange circles indicate petal primordia and petals at maturity, blue circles represent stamen primordia and stamens in the mature flower, light blue circles represent stamen primordia that will cease development. Development is illustrated with three stages from left to right. The top and middle example show the development of two flowers with different androecia (i.e., the male reproductive organs) arising from the same initial developmental stage. The middle and bottom example show the development of two flowers with an identical androecium configuration arising from different initial developmental stages. These examples highlight the importance of studying flower development to fully understand the evolution of an organism or structure. The photograph of the mature flower (*Balbisia weberbaueri*, Vivianiaceae, Geraniales; Botanic Garden Berlin, 107-23-03-14/2) on the right illustrates the configuration of the upper schematic flower. Stamens, petals, and a small visible part of the gynoecium (i.e., female reproductive organs) are labeled.

understanding of life on our planet. Morphological methods and concepts should be an integral part of the training of every biology student to counter the current lack of skills in comparative morphology. There are, and have been, initiatives dedicated to promoting knowledge of morphology among students, scholars, and also the general public. Examples include the Distributed European School of Taxonomy with a variety of courses related to taxonomy and morphology (https://cetaf.org/explore/dest-distributed-school-of-european-taxonomy/), the summer courses at the Arnold Arboretum (https://arboretum.harvard.edu/research/programs-and-opportunities/summer-short-course/), the eFlower project (https://eflower.myspecies.info/), and the Flo-Re-S group (https://flores-network.com/who-we-are/; Bull-Hereñu et al., 2016), all with international workshops. These initiatives are important, but they cannot replace a solid basic education. Furthermore, basic and advanced training in comparative morphology at universities, as well as public courses, require adequate mentoring and sufficient funding by institutions and funding agencies.

Collaboration among comparative morphologists in the international community is crucial to raise awareness about the significance of morphology for other disciplines. A first initiative to raise awareness could be to organize workshops and symposia, both within and outside the context of large conferences such as the International Botanical Congress or the annual meeting of the Botanical Society of America. However, it is important to design and promote such events to nonmorphologists. A second initiative could be to create freely accessible online courses on comparative morphology and its significance, targeted at a wide audience with a general interest in the subject. Additionally, it is essential to maintain or reintroduce morphology courses in academic educational programs and fill any open positions due to retirements, or create new positions with a strong emphasis on morphology.

In short, comparative morphology is an important science in its own right, unlocking many of the remaining mysteries of evolution. It connects to several different fields of study and provides students and scientists with an important (and necessary) skill set for diverse disciplines. Further erosion of morphological knowledge will have serious consequences for many societal issues related to climate change, sustainable agriculture, and a stable life support system. To combat the decline in knowledge and expertise in comparative morphology, more positions and dedicated funding for morphological research are urgently needed. While biological knowledge has seen significant advancements in recent decades, giving rise to many exciting new disciplines, the imminent threat to comparative morphology necessitates immediate action. There is still a lot to learn from morphology.

AUTHOR CONTRIBUTIONS

J.J. and E.S. conceived the idea and wrote the article together.

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