Bio-inspired life-like motile materials systems: Changing the boundaries between living and technical systems in the Anthropocene

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Abstract
A current trend observed in the Anthropocene is the search for bioinspired solutions. Since it became possible to change the quality of the boundary between living and technical systems, more and more life-like technical products have been developed in recent years. Using five plant-inspired developments of motile technical systems for architecture and soft-robotics, we show how the boundary between living and technical systems undulates, shifts, perforates, blurs, or dissolves with increasing life-likeness. We discuss what causes theses changes in the boundary and how this contributes to the overall aim to achieve higher resilience, robustness, and improved esthetics of plant-inspired products. Inspiration from living systems that make efficient and economic use of materials and energy and are fully recyclable after “service time” may additionally contribute to sustainable material use, one of the major challenges in the Anthropocene.

Keywords
artificial Venus flytrap, biomechanics, biomimetics, boundary, cellular actuator, façade shading, Flectofin, Flectofold, life-likeness, motile systems

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Introduction

Life-like developments

Recent developments in bio-inspired materials research have aimed at creating technical materials systems and structures that exhibit more and more life-like functions. These life-like functions include mimicking their biological concept generators, both in terms of performance, robustness and resilience, and in terms of the evolutionarily favored economical use of material and energy both in “production” and “operation” (Knippers et al., 2019; Speck and Speck, 2019b; Vincent, 2002). In the following, we present five novel plant-inspired motile systems for applications in architecture, soft robotics, and other fields of technology. We compare their degree of life-likeness by considering their adaptivity and motility with focus on the translation of the underlying motion pattern and actuation, the speed of motion, the capability of sensing environmental stimuli, energy-autonomy, and the natural appearance. Whether these developments can be considered life-like systems that undulate, permeate, shift, or dissolve the boundary between living and technical systems is a question that remains to be answered individually for each innovation (Speck and Speck, 2021). Starting point is a straight and impermeable boundary between nature and culture in general, and biology (= living organisms from the present and from fossil record) and technology (= inanimate human-made world) in particular. This straight boundary does not allow any biomimetic developments. By transferring one functional principle from a biological model, the boundary becomes undulated, thereby selectively creating niches to achieve a targeted function of the biomimetic product. The transfer of multiple functional principles permeates the boundary so that the desired functions can be merged into one multifunctional biomimetic product. The transfer of a biological algorithm shifts the straight boundary toward technology, whereas the application of the biomimetic algorithm shifts and undulates the boundary creating niches with biomimetically optimized products. In an envisaged future situation where biology and technology merge completely, there should be additionally a strong focus on more sustainable products.

Contribution to sustainability

This interplay of nature and culture is a research area typical for the Anthropocene, a term that Crutzen and Stroemer (2000) proposed for the human-dominated epoch. Nowadays the Anthropocene is characterized at least by (1) the accumulation of anthropogenic deposits, (2) the “Great Acceleration,” namely the exponential increase of human-induced effects and simultaneously the exponential decrease of biodiversity (Steffen et al., 2011), and (3) the human-induced proximity to the tipping point of global warming. With the perception of the global problems that humankind should solve in the Anthropocene, calls for bio-derived solutions could be heard. The flow of ideas from nature in the form of closed-loop cycles, recyclability, and energy efficiency seems to promise simple solutions. However, technical products are not sustainable simply as a by-product of having a biological model (Speck et al., 2017). However, practitioners can only guarantee a contribution of bio-inspired developments to sustainable development if a respectful interaction with the natural environment and a special ethos complement their technological ambitions (MacKinnon et al., 2020). With this claim, bio-inspired developments can contribute to environmental, economic, and social sustainability in the Anthropocene (Gebeshuber et al., 2009; Speck et al., 2021).

Plant-inspired technical motile systems

To start with, one may ask why plants are selected as biological models for motile technical systems since plants and plant communities seem to be rather static and apparently immobile. This misjudgment results from the finding that plant movements are often too slow, as for example
growth processes (Figure 1), or too fast, as for example motile traps in carnivorous plants (see also Figures 3d and e and 6a), to be perceptible for the human eye (Dumais and Forterre, 2012; Forterre, 2013; Poppinga et al., 2013; Skotheim and Mahadevan, 2005). The duration of movement of multicellular plants is a function of the respective organ or tissue size, defined as the smallest macroscopically moving part. Plant movement can be effected by hydraulic mechanisms (e.g. reversible shrinking and swelling of cells and irreversible growth) and/or can be sped up by the release of stored energy, initially caused by continuously built up mechanical pre-stresses (Dumais and Forterre, 2012; Skotheim and Mahadevan, 2005).

Of special importance for the transfer to plant-inspired technical motile systems is the finding that plants typically perform movements by elastic deformation of larger regions of their tissues or organs, that is without localized hinges (Forterre, 2013; Knippers et al., 2019; Körner et al., 2018; Lashi et al., 2017; Lienhard et al., 2011; Mader et al., 2020; Mazzolai et al., 2020a; Schleicher et al., 2015). This set-up avoids stress concentrations, which are typical for pivot points in conventional technical joints and reduces failure caused by overload and/or pronounced wear. Localized hinges are not only found in many technical joints but also are characteristic for many mobile animals such as arthropods and vertebrates, in which movement is based on a complex interplay of muscles (actuators), stiff members (bones or cutinized leg elements), and localized joints with gliding parts (e.g. van de Kamp et al., 2011) (Figure 2). These animals served as models for insect- or spider-inspired six- or eight-legged robots, for four-legged mammal inspired robots and two-legged humanoid robots.
Already in the 1990s with the first insect inspired six-legged robots and especially in the 2000s with the more sophisticated versions, the similarity of robotic and animal ‘motion styles’ was striking (cf. Ritzmann et al., 2004; Sequeira et al., 2016; Tedeshi and Carbone, 2014). However, motion speed, details in motion pattern, the type of actuation, and especially the used materials made it easy to recognize them as artifacts, which are hard to mix up with real insects. This changed with the development of soft robots, in which motion based on elastic deformation became dominant. Examples include soft robots inspired by octopus arms and plants and other motile systems, in which the motion pattern, the type of actuation, and the general appearance became increasingly similar to their biological models (Cezan et al., 2020; Laschi et al., 2017; Majidi, 2018; Mazzolai et al., 2020a, 2020b; Must et al., 2019; Sadeghi et al., 2020). In these structures not only the functionality of the biological models was successfully transferred, but increasingly also the underlying hierarchical structuring, the actuation principles and—perhaps most important—also the esthetics of motion patterns of the biological concept generators (Knippers et al., 2019; Speck, 2015; Speck and Speck, 2019a). Recent attempts aim at transferring additional technically interesting functions of the biological models as for example improved sensing-(re)action-coupling, (self-)adaptability, self-repair, and energy-autonomy in the next generations of bio-inspired soft robots and motile systems in general (Cezan et al., 2020; Laschi et al., 2017; Majidi, 2018; Mazzolai et al., 2020a, 2020b; Meder et al., 2020). Plants have proven to be very suitable concept generators for this task as they lack a central control unit (i.e. a brain) and most sensing and (re)acting take place decentralized in the various organs or tissues. This makes plants highly appropriate biological models for the development of novel smart-up materials systems, which are a prerequisite for the next generation of bio-inspired systems.

**Aim of the study**

In this article, we present five plant-inspired examples that were developed by the Plant Biomechanics Group of the University of Freiburg in collaboration with colleagues from the Institute of Building Structures and Structural Design as well as the Institute for Computational Design and Construction of the University of Stuttgart. Within the framework of the Cluster of Excellence *livMatS*, we examine how far these examples undulate, permeate, shift, or dissolve the boundary between living and technical systems (Speck and Speck, 2021).

**First example: Flectofin®—a façade shading system inspired by the bird-of-paradise flower**

Many flowering plants are pollinated by animals, which get a reward (typically nectar) in return. In some species, the pollen, which has to be transferred from one flower to another, is not directly accessible to the pollinating animal but rather is concealed within a specific flower structure. A well-known example for this can be found in the bird-of-paradise (*Strelitzia reginae*), a popular South African ornamental plant. Its inflorescences carry numerous flowers, which open one after another (Figure 3a). Each flower develops a conspicuous violet cylindrical sheath consisting of two fused petals. This petal sheath, which is open along its length on top, acts as a valvular structure, hiding and protecting the stamens with pollen, and exposing them only when the pollinator is present (Kronestedt and Walles, 1986) (Figure 3b). The bird-of-paradise is pollinated by birds (Rowan, 1974; Skead, 1975), which land on the flower sheath, which acts as a perch, to search for nectar reward. Due to the body weight of the animal, the sheath bends downwards and flaps open by a process known, in technical mechanics, as torsional buckling. Hereby the pollen is presented and sticks to the bird’s feet allowing for transportation to another flower. When the bird flies away, the sheath closes and the pollen is protected again. Such a valvular pollination mechanism
incorporates a completely extrinsically actuated petal movement, meaning that the motion is not driven by the plant itself but by the bird, which exerts mechanical pressure by its weight force. Self-actuated plant movements, like the folding of the *Mimosa pudica* leaves, are otherwise driven by (combinations of) various principles of hydraulic actuation (i.e. internal water displacement processes between cells and tissues) and/or the release of pre-stress stored in the motile structure (see Poppinga et al., 2013, 2018a, 2018b, 2020 for reviews).

Functional-morphological analyses of the bird-of-paradise petal sheath revealed that it consists of stiff ribs, which are connected by very thin and flexible laminae (Lienhard et al., 2011). When the sheath is deformed due to the bird’s body weight, a simultaneous sideways bending of the lateral sheath parts is initiated, leading to the opening of the structure (Figure 3b). Biomechanical analyses revealed that this movement could be repeated many times with (nearly) exactly the same force-displacement-curves and without any notable material fatigue (Masselter et al., 2018;}

**Figure 3.** Biological concept generators and the respective biomimetic façade shading systems Flectofin® and Flectofold. (a) The inflorescence of the bird-of-paradise (*Strelitzia reginae*) consists of several flowers. Each flower features a petal sheath, which acts as a perch for pollinating birds. (b) The sheath opens under the body weight of the bird (simulated here by applying mechanical pressure) and exposes the stamens with pollen. The pollen adheres to the birds’ feet and can be transported to other flowers for cross-pollination. The underlying deformation principle of the valvular sheath is torsional buckling, which is otherwise considered a failure mode in engineering. (c) The Flectofin® is a biomimetic façade shading system. Through the bending of its backbone, the lateral flaps deflect sideways by torsional buckling similar to the petal sheath of the bird-of-paradise. (Image modified from Schleicher et al., 2015). (d) The aquatic carnivorous waterwheel plant (*Aldrovanda vesiculosa*) captures small zooplankton prey with millimeter-sized snap traps. (e) The trap consists of two trap lobes and a midrib. The trigger hairs inside the trap are not visible in this image. When prey touches the trigger hairs, the very fast snapping movement is initiated. The trap closes by bending of the midrib and concomitant motion amplification caused by curved-fold bending of the two lobes. (f) A large-scale array of Flectofold systems. The Flectofold is a biomimetic façade shading element, which shows curved fold bending deformation and kinematic amplification like the Waterwheel trap. It can be applied to curved building surfaces and possesses a functional elegance similar to its biological concept generator. (©ITKE Stuttgart, modified, with kind permission)
Poppinga et al., 2010). By deconstructing the overall composite sheath architecture into its individual kinematical parts, that is, the rib-lamina elements, the underlying deformation principle could be elucidated. When individual ribs are bent, the attached laminae show a very prominent sideways flapping of up to 90° due to the aforementioned process of torsional buckling (Lienhard et al., 2011).

In a biomimetics biology push process (bottom-up-approach) (Speck and Speck, 2008), an artificial rib-laminae element made of glass fiber reinforced polymers was developed, the Flectofin® (Knippers et al., 2019; Lienhard et al., 2011) (Figure 3c). It consists of a backbone (the “rib”) carrying one or two lateral flaps (the “laminae”), which deflect by 90° upon bending of the backbone. The required bending can be initiated by applying an external mechanical force (e.g. with hydraulic bending of the backbone) or by differential thermal expansion of the backbone materials if made of laminated layers differing in thermal expansion. In order to avoid notch stresses during torsional buckling-induced sideways flapping, edge reinforcements were implemented into the flaps and a contour geometry optimization was applied. The Flectofin® is a biomimetic, hinge-free façade shading element capable of continuous and smooth opening and closing cycles. Due to a minimal amount of individual constructional parts, the mechanical complexity of this system could be drastically reduced compared to typical technical blinds or louvers. Furthermore, the deformation principle is scalable and can be applied to small-scale microsystems as well as large-scale architectural building components if a suitable length-to-width ratio of the Flectofin® elements is kept (Schleicher et al., 2015).

Torsional buckling is considered a failure mode in engineering (Trahair, 1993), yet it is “utilized” in a flower for achieving compliance. The successful implementation of such natural failure modes into technical systems can be considered a paradigm shift and can lead to an enhanced “methods toolbox” for developing compliant systems. Based on further abstraction processes, an up to 13 m long deployable louver system was developed and built for the thematic pavilion at the 2012 EXPO in Yeosu, South Korea (Knippers et al., 2012, 2019). The bio-inspired kinematic façade of the thematic pavilion in Yeosu is very well accepted by the public and has gained much attention worldwide.

In this bio-inspired kinematic façade, the bending—causing opening and closing—of the individual elements is effected by hydraulic pistons at the base of each element, that is by a conventional technical actuation method, which applies considerably high pressures. It can be clearly identified as bio-inspired, functionally robust and in its life-like motion pattern a very aesthetic solution but nevertheless it definitively represents a technical structure. By transferring the functional principle of torsional buckling, the boundary between biology and technology becomes undulated, creating niches in which the targeted function, that is plant-inspired façade-shading, of the Flectofin® is fulfilled.

Second example: Flectofold—a façade shading system inspired by the motion of the underwater snap trap of the waterwheel plant

As further biological concept generator for a kinetic façade shading system served the aquatic carnivorous waterwheel plant (*Aldrovanda vesiculosa*) (Figure 3d), which is a close relative of the (in)famous Venus flytrap (*Dionaea muscipula*) (see fourth example). In contrast to *Dionaea*, the waterwheel plant develops millimeter-sized snap traps underwater (Figure 3e), which allows for the capture of a wide range of aquatic prey animals as a substantial nutrient supply, for example, water fleas, snails, and water mites (Horstmann et al., 2019). When prey enters the trap and touches the trigger hairs situated on the inner surface, an electrical signal is generated, which elicits the very fast snapping motion and capture of the animal (Ashida, 1934; Poppinga et al., 2019).
The trap consists of two lobes, which are connected by a midrib (Figure 3e). Each lobe possesses a convex (outwards) curvature, as seen from outside, which does not change during trap closure. The snapping of the *Aldrovanda* incorporates a complex interplay of different actuation and folding principles and, therefore, constitutes a self-actuated motion. After being triggered by prey, initially turgid motor cells situated close to the midrib become flaccid by losing their turgor pressure (Ashida, 1934; Westermeier et al., 2020). The midrib, which is straight and prestressed when the trap is open, can thereby relax and bend inwards (Westermeier et al., 2018). Due to kinematical coupling with the midrib, the two attached lobes synchronously move toward each other until the trap is shut (Poppinga and Joyeux, 2011; Westermeier et al., 2018). In this state, when the prey is caught, the midrib shows a very pronounced bending deformation and the two lobes press against each other. The snapping duration depends on the temperature but is very fast with a duration of typically 10–100 ms (Westermeier et al., 2018). After closure, the forming of a digestion chamber starts, which takes a few hours to complete and leads to a further narrowing of the trap and a concomitant reduction of the interior volume by ~90% (Ashida, 1934; Westermeier et al., 2020). Then a cocktail of digestive enzymes is released and the prey becomes digested, after which the trap reopens and is ready for another snap.

The waterwheel trap constitutes a single kinematic element (a bendable midrib with kinematically coupled lobes) and always moves as a global structure with a smooth continuous motion pattern. This is in contrast to the Venus flytrap, whose traps consist of two individually actuated lobes (Forterre et al., 2005; Sachse et al., 2020), which may move asynchronously by curvature inversion, that is snap buckling (Poppinga et al., 2016) (see also fourth example).

In the framework of a biology push process (bottom-up-approach) in biomimetics (Speck and Speck, 2008), the waterwheel trap has proven to be a very promising concept generator for the development of functionally resilient biomimetic compliant motile systems. The underlying geometric motion principle was successfully abstracted and transferred into a simplified curved-line folding geometry with distinct flexible hinge-zones. This abstracted model represented the basis for a transfer into a technical structure made of glass fiber reinforced plastics. The structure and setup of the curved folds were further optimized by using inspiration from the wing folding of the Italian striped bug (*Graphosoma italicum*), which enabled the Flectofold to avoid fatigue in an area subject to particular mechanical stress thus increasing the service life (Knippers et al., 2019; Körner et al., 2018). A one-dimensional actuation force (e.g. by pneumatic cushions with low actuation pressure in the range of 0.004–0.006 MPa) with comparatively small initial bending deformation of a backbone (the “midrib”) leads to a pronounced three-dimensional global response of the whole kinetic structure, that is opening or closing of the kinematically coupled lateral membranes. The resulting biomimetic compliant system, the Flectofold (Körner et al., 2018; Saffarian et al., 2020), can be applied as a shading element for complex free form façades, covering all types of clinal and anticlinal surfaces without any gaps. The Flectofold elements are initially square, scalable and are distortable in geometry, but still remain fully functional. Additionally, the Flectofold shows a striking functional elegance (natural appearance) (Figure 3f), an often overlooked value in biomimetic applications (Speck, 2015; Speck and Speck, 2019). From an exhibition in the Museum for Natural History in Stuttgart (see Virtual Exhibition Tour, 2020) we know that the Flectofold façade shading system is very well accepted by the public.

The development of the Flectofold changes the border between living and technical systems through both the transfer of a plant-inspired motion pattern and a first attempt for a more plant-inspired actuation. The use of the low pressure in the soft pneumatic cushions much more resembles the pressure generation mechanisms in plants. Its plant-inspired actuation mode not only increases the quantity of plant-inspired functions, but due to its actuation by low-pressure pneumatic cushions also the life-like quality, and by this, deeper undulates the boundary between
biology and technology. Moreover, its aesthetic motion pattern is even more reminiscent of the biological model than the motion pattern of Flectofin®.

**Third example: Cellular actuator—kinetic amplification triggered by plant-inspired motor cells**

The biomimetic cellular actuator was developed in a typical technology pull process (top-down process) of biomimetics (Mader et al., 2017, 2020; Speck and Speck, 2008). The challenge was to create a plant-inspired actuator for compliant systems in the building sector. A first application was the façade shading element Flectofold, a biomimetic compliant kinetic element inspired by the hinge-less motion of the underwater trap of the carnivorous waterwheel plant (see second example for details) (Körner et al., 2018). Similar to buildings, which are typically immobile as a whole but possess individual motile components like doors and blinds, plants also develop individual kinematic plant parts (leaves, petals, seed capsules, etc.). These biological compliant systems can act as concept generators for the development of biomimetic technical structures for architecture.

Inspiration for the cellular actuator were the hydraulically driven movements of grass leaves. The actuators of the kinetic amplification are the motor cells, also called bulliform cells. They represent enlarged epidermal cells on the adaxial (= upper) side of the leaf, forming groups of approximately 10 cells. If the bulliform cells are concentrated at the midrib, the leaf halves open at high turgor pressure of the motor cells and close at low turgor pressure. The structural integrity of the leaf during motion is ensured by abutments, which consist of vascular bundles and sclerenchyma strands between the adaxial (= upper) epidermis and abaxial (= lower) epidermis (Figure 4) (Betz et al., 2016; Mader et al., 2017, 2020). Morphometric parameters of the bulliform cells as
well as opening angles of fresh and dried leaf halves were taken from *Sesleria nitida*, a species belonging to the grass family (Poaceae) (Mader et al., 2020).

As a prerequisite for the technical implementation, a finite-element analysis of the leaf movements triggered by bulliform cells was carried out. This analysis focused on the geometry of the leaf, the geometry of the bulliform cells in turgescent and non-turgescent states, and the opening angles of the two leaf halves in turgescent and non-turgescent states. The simulation for the biological model showed an almost linear relationship between turgor increase in the bulliform cells and increase of the opening angle between the two leaf halves. Based on these findings, artificial cells made of glass-fiber-reinforced epoxy composites (GFRP) were constructed for the plant-inspired cellular actuator. Dependent on the cell geometry and various wall thicknesses, an increase of the air pressure inside the cell causes the vertical sidewalls to tilt outwards if cell wall thickness is varied as shown in Figure 5. A numerical simulation shows that the sidewall angle increases with increasing internal cell pressure. Since the cellular actuator consists of a row of such pneumatic cells fixed to a plate, the tilting of the cell sidewalls under compressed air causes the entire structure to bend (Mader et al., 2020).

The bio-inspired façade shading system Flectofold was selected to prove the functionality of the cellular actuator as a bending actuator. A single row of pneumatic cells in the midrib of Flectofold is sufficient for a self-contained system that is able to open and close without an additional supporting substructure. For actuating the small-scale Flectofold to an opening angle of 90°, an angular deflection of the cell sidewalls of 4.7° was required, which was reached at an internal pressure of 0.02 MPa (Mader et al., 2020).

In summary, a biomimetic actuator consisting of pneumatic cells was developed after gaining inspiration from the kinetic amplification of the opening and closing movement of the grass leaf, which depends on the turgor changes of the bulliform cells. Key parameters from the biological model ensure the transfer of the functional principles to achieve the desired function. These parameters include the cellular design and cell wall structure, the fluid-mediated volume change of motor cells, and the reversible movement of the entire component. In order to adapt functions from a living model to an artificial product, some abstractions were, however, necessary: from a folding of the leaf halves to a bending of the cellular actuator, from a hydraulically driven movement caused by the turgor pressure in motor cells to a pneumatically driven movement caused by pressurized air in technical cells, and from a fan-shaped group of bulliform cells on the upper side of the leaf to a row of technical cells with an asymmetric geometry and wall thickness.

The transfer of multiple functional principles is possible through the permeability of the boundary between living organisms and technical systems that allows for merging of the functional principles within a multifunctional biomimetic product. In this case, the motion principle inspired by the trap of the waterwheel plant, was transferred to the Flectofold. Additionally, the actuation principle of bulliform cells of grass leaves was realized in the cellular actuator. The actuation by a row of cells in contrast to the previously used single pneumatic cushion allows for a more finely tuneable motion pattern and a more reliable actuation. By designing a multifunctional biomimetic product, we increased the life-like quality of the entire system.

**Fourth example: The Venus flytrap as concept generator for plant-inspired soft robots (AVFT: artificial Venus flytrap)**

As mentioned above, plants are particularly interesting for low energy and very reliable motion systems as for example in façade shading systems (Knippers et al., 2019; Körner et al. 2018; Schleicher et al. 2015) (see first and second example for details). Through the combination of the movement during prey capture of two carnivorous plant species *Dionaea muscipula* (Venus
flytrap) (Figure 6a) and *Aldrovanda vesiculosa* (waterwheel plant) (cf. Figure 3d and e) novel plant inspired soft robotic motion systems have been developed. So far, *D. muscipula* has already inspired a number of different biomimetic systems and robots throughout the last 25 years (Esser et al. 2019, 2020) (Figure 6b–e), and *A. vesiculosa*, which gave the inspiration for the Flectofold system.

The movement of both plants are among the fastest in the plant kingdom. *A. vesiculosa*, the phylogenetic sister species to the *D. muscipula*, closes its traps within 10–100 ms. Its movement is driven by active hydraulics, elastic relaxation of the midrib, and kinematic amplification (Ashida, 1934; Poppinga and Joyeux, 2011; Westermeier et al., 2018). In contrast, the *D. muscipula* employs an initial hydraulic deformation through water displacement followed by the release of stored elastic energy, leading to the fast closing movement of the trap lobes within 100–300 ms (Forterre et al., 2005; Poppinga and Joyeux, 2011; Poppinga et al., 2018a; Sachse et al., 2020; Westermeier et al., 2018).

*D. muscipula* produces up to ten leaves with approximately 2 cm long traps, each consisting of two lobes connected via a midrib (Figure 6a). Each lobe has three to four trigger hairs present on the inside. Trap closure is typically triggered when prey stimulates at least one of the trigger hairs inside the trap twice within a certain time frame (20–30 seconds at room temperature) (Hodick and Sievers, 1989). However, also a slow single deflection of a trigger hair by prey can be in individual cases enough to trigger the trap (Burri et al., 2020). Within the trap tissue a change in calcium levels is responsible for memorizing stimuli and transducing the signal to the effector cells (Suda et al., 2020). Open and ready-to-snap trap lobes have a typical concave spatial curvature (as seen from the outside) and undergo rapid curvature inversion while releasing the stored energy (snap buckling) during closing. Therefore, the lobes are described as bi-stable systems with two low-energy states (Poppinga and Joyeux, 2011; Sachse et al., 2020). After successful prey capture and digestion, a

![Figure 5](image-url)
re-opening of the traps occurs over 1–2 days (Fagerberg and Howe, 1996; Poppinga et al., 2016; Volkov et al., 2014). The trap opening is driven by irreversible growth processes (Ashida, 1934) and/or by hydrostatic pressure changes within the lobes (Markin et al., 2008).

As mentioned above over the last 25 years, the motion principles of the Venus flytrap have repeatedly been in the focus of research for the development of bio-inspired and biomimetic artificial Venus flytrap (AVFT) robots (Esser et al., 2020). Plants do not have a central control unit for

Figure 6. Overview of current state of the art AVFT systems categorized by actuation mode. (a) The images show the biological model D. muscipula in an open and closed state. The trap consist of two lobes and a midrib. The fast snap buckling trap closure movement is typically initiated when prey deflects the trigger hairs twice within a certain time. The Venus flytrap morphology, as well as the underlying principles were abstracted and transferred into the presented AVFT systems. (b) Electromagnetic systems: (1) Electromagnetic Carbon fiber reinforced polymer-based AVFT, the magnet triggers lobe curvature inversion (Zhang et al., 2016); (2) Foil-based AVFT closure is realized through magnet deflection and geometrically coupled foil displacement (Esser et al., 2019) (Blue (S) and red (N) indicate magnet poles). (c) Joule heating and temperature change driven systems: heat-driven shape memory alloy (SMA)-based AVFT, where contracting springs trigger the lobe curvature inversions (Kim et al., 2014); (2) Foil-based AVFT closure is temperature-activated through utilization of a SMA spring as actuator (Esser et al., 2019). (d) Humidity driven systems: (1) Hydrogel-based, solvent-triggered doubly curved system (Lee et al., 2010); (2) Combination of two stimuli (heat/moisture) triggers the initialization of the foil-based AVFT (Esser et al., 2019). (f) Pneumatic system: (1) Silicone-based AVFT with a doubly curved lobe system. A bi-stable trigger unit releases stored energy to initiate lobe movement via snap-buckling (Pal et al., 2020); (2) Pneumatically driven foil-based AVFT. The actuation unit integrates three pneumatic cushions, an outer one for closing the “trap,” and a central one for snapping the system open through snap-buckling the backbone (Esser et al., 2019). (Image modified from Esser et al., 2020; with permission.)
decision-making and motion control, which makes them ideal biological models for technical
decentral controlled autonomous systems. First AVFT systems were driven by electric motors
(Yang et al., 2012), but as technology progressed, novel smart materials were used. Thereby,
AVFTs became even more life-like, being able to be triggered, actuated by, and react to various
environmental stimuli for example light, heat, and humidity changes. The smallest systems are
based on liquid crystal elastomers and are only a few millimeters in size (Kohlmeyer and Chen,
2013; Wani et al., 2017). Amongst other systems, these were driven by photo-thermally produced
heat (Dong et al., 2020; Lim et al., 2017) or via joule heating (Kim et al., 2014; Lim et al., 2017)
(Figure 6b). Furthermore, AVFT systems exist, in which the “trap” closure movements are actuated
via magnetism (Esser et al., 2019; Schmied et al., 2017; Zhang et al., 2016) (Figure 6c), electricity
(Shahinpoor, 2011; Shahinpoor and Thompson, 1995), pressurized air (Esser et al., 2019; Pal et al.,
2020; Temirel et al., 2016; Wang et al., 2020) (Figure 6d), temperature changes (Esser et al., 2019;
Riley et al., 2020) (Figure 6b), or hydrogel swelling or shrinking activated via enzymes (Athas
et al., 2016) or moisture (Esser et al., 2019; Fan et al., 2019; Lee et al., 2010; Zhu et al., 2020)
(Figure 6e).

An extensive overview of current AVFT system is given in the review article of Esser et al.
(2020), in which they were categorized depending on their actuation mode and compared to the
biological model in terms of sensing capabilities, snap-buckling, lobe closure time, requirements
for actuation, and movement reversibility. Most of the AVFT systems only react to stimuli by clos-
ing their traps, but only a few adapt and also look similar to the biological model (Figure 6e).

The compliant foil snap trap demonstrator developed by Esser et al. (2019) is considered a cur-
rent base line AVFT system for actuation and reaction to stimuli (Figure 6b2–e2). The basic snap-
trap geometries of D. muscipula and A. vesiculosa (Sachse et al., 2020; Westermeier et al., 2018,
2019), which were abstracted and transferred into a compliant foil AVFT demonstrator resembling
in appearance the snap trap mechanisms of the two plants models. By means of different types of
actuation (magnetically, thermally, pneumatically, and by a combination of temperature and humid-
ity change), an intrinsic actuation of the demonstrator similar to the biological model can be
achieved (Figure 6b2–e2). In the case of the temperature-humidity-triggered system even, an
intrinsic-hydraulic and energy-autonomous actuation is realized through a combination of hydro-
gel and shape memory polymer resembling more and more the biological model.

Artificial Venus flytraps are a prime example of building technical systems that mimic their
biological concept generators as closely as possible without focusing on technical use as a main
goal. In the presented feasibility studies, the scientists try to find out to which extend a complex
biological system can be designed with purely technical materials and approaches. Until now, none
of the artificial Venus flytraps has incorporated all relevant functional principles to make them
indistinguishable from the biological model. For a transfer of all essential functions of the living
D. muscipula into a life-like artificial Venus flytrap a system has to be developed that is able to
snap and move like the biological model. It has to be able to sense its environment, to make a
decentralized decision on whether or not to capture “prey,” to harvest energy-autonomously from
the environment, and finally it must be capable of self-repair (Esser et al., 2020). Today’s existing
artificial Venus flytraps and the described compliant demonstrator already permeate the boundaries
between biology and technology. They resemble the biological model in natural appearance,
motion patterns, and (at least partly) achieving energy-autonomy through environmentally driven
intrinsic actuators. However, these feasibility studies done so far are still far from removing the
boundaries to an extent that makes it impossible to tell whether a system is artificial or a living
organism by considering its functionalities.
Fifth example: Weather-responsive building skins with autonomous actuation inspired by the hygroscopic movement of pine cone scales

For plants with wind-dispersed (anemochorous) fruits or seeds it is advantageous to release the fruits/seeds when it is dry, which enhances the probability that they are effectively dispersed by the wind. The woody seed cones of pines (*Pinus* spp.), which contain the airborne seeds, are prime examples for such weather-responsive dispersal structures. What makes them particularly interesting for biomimetics is the fact that the cone opening movements involved in the seed release are independent to the plant’s metabolism and run energetically “for free.” They are completely passively driven by changes of environmental humidity and based on different swelling properties of hygroscopic tissues (Correa et al., 2020; Elbaum, 2018; Elbaum and Abraham, 2014).

The pine cone consists of a multitude of seed scales, which are spirally arranged around a central cone axis (Shaw, 1914) (Figure 7a). In a humid/wet environment, when the cone is closed and the seeds are locked in the cone and protected, each scale is bent upwards. In a dry environment, the scales are bent downwards, the pine cone is open, and the wind has access to the seeds, which can then be transported away ensuring dispersal (Figure 7a and b). The functional scale morphology and anatomy allowing for such completely reversible bending deformation has been analyzed for over a century (Allen and Wardrop, 1964; Harlow et al., 1964; Le Duigou and Castro, 2016; Reyssat and Mahadevan, 2009; Shaw, 1914) and has often been compared to the structural setup of a bimetallic strip consisting of two metals with different thermal expansion coefficients. In contrast to the bimetallic strip, which bends when the temperature changes (Timoshenko, 1925), the cone scales show humidity-dependent bending. This is because the two main cone scale tissue layers, that is, the sclereids and sclerenchyma, possess different swelling properties and together constitute a functional moisture-sensitive bilayer. The sclereids are highly swellable and, upon water uptake, expand by ~20% in the longitudinal direction of the scale (Reyssat and Mahadevan, 2009). Thereby, they function as the actuating layer and drive the scale motion. In contrast, the sclerenchyma cells do not swell much. They act as a mechanical resistance layer and dictate the directions of the bending deformation. The roles of the other tissue layers, for example, the epidermis with cuticle and “brown tissue” matrices (sensu Shaw, 1914), are not well understood so far and are subject to ongoing research. Seed scale movement has even been documented from fossilized cones that are millions of years old (Poppinga et al., 2017). This highlights the extremely high functional resilience and robustness of these energy-autonomous hygroscopic structures.

The pine cone seed scale is a frequently used biological concept generator in biomimetics for approaches that deal with the development of smart and autonomous actuators. The underlying bilayer architecture can be mimicked with various artificial and natural materials and allows for fine-tuning the triggering sensitivity and the overall mechanical response of the structure. With the help of such advanced materials systems, responses to changes in humidity, temperature, light, and pH, for example, are possible (Bargardi et al., 2016; Erb et al., 2013; Ionov, 2014). Novel 4D printing methods allow for the development of advanced actuator systems with complex geometries and motion patterns. The structural programming of shape-changing 4D prints has become an emerging field of research (Gladman et al., 2016). Recently, the complex two-phase and biaxial motion of the Bhutan pine (*Pinus wallichiana*) cone scale was successfully transferred into 4D printed biomimetic scale-like flaps, which consist of co-polyester with embedded cellulose fibrils (constituting the actuating layer) and resistance ABS (acrylonitrile butadiene styrene) plastic layers (Correa et al., 2020) (Figure 7c). Additionally, other biomimetic 4D prints, which are capable of complex deformation patterns known from plants, for example, snap-buckling and curved fold origami, have been developed (Poppinga et al., 2020). The successful technical implementation of
these versatile motion principles demonstrates the high potential of plant movements for biometrics. Despite the purely passive actuation principle, spatially complex, multi-step, and almost life-like motions can be achieved.

The pine cone scale-inspired 4D printed biomimetic scale-like flaps show a very life-like motion pattern. Moreover, concerning the intrinsic hygroscopic actuation, the artificial flaps are also in this regard very similar to their biological concept generators. Additionally, the plant-inspired structural setup allows for going beyond biology by not only using humidity changes as actuating agent but also changes in temperature, light, or pH, depending on the stimulus to which the actuating layer used is sensitive (Bargardi et al., 2016; Erb et al., 2013; Ionov, 2014).

Pine cone scale-inspired 4D printed biomimetic scale-like flaps can be considered as life-like materials systems in which the boundary between living and technical systems has been permeated and nearly removed. The artificial flaps can be produced in a way that makes them structurally as well as functionally (nearly) indistinguishable from their biological models without including living or other biological material.

**Comparison of life-likeness in the presented examples**

The presented five plant-inspired motion systems can be considered as examples in which the integration of the criteria of life-likeness results in an increase in life-likeness (Table 1). Key for a successful transfer of functional principles from the plant models to the technical products is the abstraction and translation of the underlying structures. This has been made possible by improved manufacturing processes that allow engineering to construct from small to large in a manner similar to biology, that is, to build hierarchically structured material systems. Based on the number of
criteria that are fulfilled, the degree of like-likeness with focus on adaptivity and motility can be estimated: translation of the underlying principles of deformation and actuation, speed of motion, sensing of environmental stimuli, energy-autonomy, and natural appearance.

First, a lifelike movement pattern (natural appearance) is achieved by integrating the kinematic movement principle into the Flectofin® system. The Flectofold further undulates the boundary between living and technical systems by implementing not only a bioinspired motion pattern but also a more plant-inspired actuation mode. The combination of cellular actuator and Flectofold presented in the third example matches the biological model even better by integrating a fine-tuneable more reliably actuating cellular system into the Flectofold, thereby permeating the boundary between biology and technology and increasing its life-likeness even further. In the case of the fourth example (AVFT), the compliant foil demonstrator combines two motion principles of snap traps, going beyond the biological models. The artificial Venus flytraps are characterized by a very life-like motion pattern and can even move faster than the biological models. They resemble the biological models in natural appearance, motion pattern, reactivity, adaptability and (partial) energy-autonomy, and by this, the AVFTs permeate and partly remove the boundaries between biology and technology. An especially life-like biomimetic system is shown in the fifth example (4D-printed scale), produced by additive manufacturing. It represents a compliant system, almost indistinguishable from the biological model. A truly life-like materials system is achieved by implementing the plant-inspired motion principle actuated by a hygroscopic material, integrated sensing and acting capabilities, and a very natural appearance. In this example, the boundary between living and technical systems is removed.

**Conclusion and outlook**

In the Anthropocene, a human-dominated epoch, there is a current trend of returning to nature and searching for bio-derived solutions. Novel methods of analysis and production are making it possible to overcome the boundaries between biology and technology more and more. The five plant-inspired developments presented exemplify the change of quality of the boundary resulting in an increasing degree of life-likeness of technical products. These developments may be considered as life-like systems that undulate, permeate, shift, or dissolve the boundary between living and technical systems (cf. Speck and Speck, 2021). Typically, increasing life-likeness is not the primary goal of bio-inspired developments, but rather is a consequence of integrating more and more functional principles of biological concept generators into bio-inspired products.

Since a contribution to sustainable material use is one of the major challenges and goals in the Anthropocene, taking inspiration from living systems that make efficient and economic use of materials and energy, are multi-functional, and fully recyclable after “service time” could provide additional valuable inputs for a greener future. However, increasing life-likeness may cause fear in

| Examples                | Criteria of life-likeness | Motion pattern | Speed of motion | Actuation | Sensing | Energy-autonomy | Natural appearance | Life-likeness |
|-------------------------|---------------------------|----------------|-----------------|-----------|---------|-----------------|-------------------|--------------|
| Flectofin®              | ✓                         | —              | —               | —         | —       | (✓)             | ✓                 | ✓            |
| Flectofold              | ✓                         | —              | —               | (✓)       | —       | —               | ✓                 | ✓            |
| Cellular actuator       | ✓                         | —              | ✓               | —         | —       | —               | ✓                 | ✓            |
| Compliant AVFT          | ✓ ✓                       | ✓              | ✓               | (✓)       | —       | (✓)             | ✓                 | ✓ ✓          |
| 4D-printed scale        | ✓ ✓ ✓ ✓                   | ✓              | ✓               | ✓         | ✓       | ✓               | ✓                 | ✓ ✓ ✓         |
✓: equal to the biological model; (✓): similar to the biological model; —: differs from the biological model.
users due to less or even a loss of control over self-sufficient technical products. Deciding how to handle novel possibilities and problems may become one of the most controversial issues concerning the development of bio-inspired materials and systems within the Anthropocene. Such fundamental discussions are all the more to be expected when self-reproducibility comes into play as a central aspect of life, an aspect that we have deliberately excluded in our above-mentioned considerations and in the framework of our bio-inspired developments. The aspect and effects of increasing life-likeness will be studied in the example of the artificial Venus flytrap. The various versions of artificial Venus flytraps we are currently developing will have an increasing number of life-like features (except self-reproducibility) and by this will allow for testing the degree of life-likeness. Furthermore, in cooperation with our colleagues from the social sciences, the diverse versions of the artificial Venus flytraps have already been selected to test the extent to which it finds societal acceptance among technical users and the public as it gains increasing life-likeness.

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References

Allen R and Wardrop AB (1964) The opening and shedding mechanism of the female cones of Pinus radiata. Australian Journal of Botany 12(2): 125–134.
Ashida J (1934) Studies on the leaf movement of Aldrovanda vesiculosa L. Memoirs of the College of Science; Kyoto Imperial University Series B 9: 141–244.
Athas JC, Nguyen CP, Zarket BC et al. (2016) Enzyme-triggered folding of hydrogels: Toward a mimic of the Venus flytrap. ACS Applied Materials & Interfaces 8(29): 19066–19074.
Bargardi FL, Le Ferrand H, Libanori R et al. (2016) Bio-inspired self-shaping ceramics. Nature Communications 7: 13912.
Betz O, Birkhold A, Caliaro M et al. (2016) Adaptive stiffness and joint-free kinematics – Actively actuated rod-shaped structures in plants and animals and their biomimetic potential in architecture and engineering. In: Knippers J, Nickel K and Speck T (eds.) Biomimetic Research for Architecture and Building Construction: Biological Design and Integrative Structures. Bio-inspired Systems, vol. 9. Cham: Springer, pp.135–167.
Burri JT, Saikia E, Laübli NF et al. (2020) A single touch can provide sufficient mechanical stimulation to trigger Venus flytrap closure. PLoS Biology 18(7): e3000740.
Cezan SD, Bayssekin HT and Baytekin B (2020) Self-regulating plant robots: Bioinspired heliotropism and nyctinasty. Soft Robotics 7(4): 444–450.
Correa D, Poppinga S, Mylo MD et al. (2020) 4D pine scale: biomimetic 4D printed autonomous scale and flap structures capable of multi-phase movement. *Philosophical Transactions of The Royal Society A* 378(2167): 20190445.

Crutzen PJ and Stoermer EF (2000) The “Anthropocene”. *Global Change Newsletter* 41: 17–18.

Dong X, Xu J, Xu X et al. (2020) Sunlight-driven continuous flapping-wing motion. *ACS Applied Materials & Interfaces* 12(5): 6460–6470.

Dumais J and Forterre Y (2012) Vegetable dynamicks: The role of water in plant movements. *Annual Review of Fluid Mechanics* 44(453): 453–478.

Elbaum R (2018) Structural principles in the design of hygroscopically moving plant cells. In: Geitmann A and Gril J (eds.) *Plant Biomechanics*. Cham: Springer, pp.235–246.

Elbaum R and Abraham Y (2014) Microstructures of hygroscopic movement devices in plant seed dispersal. *Plant Science* 223: 124–133.

Erb RM, Sander JS, Grisch R et al. (2013) Self-shaping composites with programmable bioinspired microstructures. *Nature Communications* 4: 1712.

Esser FJ, Auth P and Speck T (2020) Artificial Venus flytraps: A research review and outlook on their importance for novel bioinspired materials systems. *Frontiers of Robotics and AI* 7: 75.

Esser F, Scherag FD, Poppinga S et al. (2019) Adaptive biomimetic actuator systems reacting to various stimuli by and combining two biological snap-trap mechanics. In: Martinez-Hernandez U, Vouloutsi V, Mura A et al. (eds.) *Biomimetic and Biohybrid Systems. 8th International Conference*. Cham: Springer, pp.114–121.

Fagerberg WR and Howe DG (1996) A quantitative study of tissue dynamics in Venus’s flytrap *Dionaea muscipula* (Droseraceae). II. Trap reopening. *American Journal of Botany* 83(7): 836–842.

Fan W, Shan C, Guo H et al. (2019) Dual-gradient enabled ultrafast biomimetic snapping of hydrogel materials. *Science Advances* 5(4): eaav7174.

Forterre Y (2013) Slow, fast and furious: Understanding the physics of plant movements. *Journal of Experimental Botany* 64(15): 4745–4760.

Forterre Y, Skotheim JM, Dumais J et al. (2005) How the Venus flytrap snaps. *Nature* 433: 421–425.

Gebeshuber IC, Gruber P and Drack M (2009) A gaze into the crystal ball: Biomimetics in the year 2059. *Proceedings of the Institution of Mechanical Engineers, Part C: Journal of Mechanical Engineering Science* 223: 2899–2918.

Gladman AS, Matsumoto E, Nuzzo R et al. (2016) Biomimetic 4D printing. *Nature Materials* 15: 413–418.

Harlow WM, Côté WA and Day AC (1964) The opening mechanism of pine cone scales. *Journal of Forestry* 62(8): 538–540.

Hodick D and Sievers A (1989) On the mechanism of trap closure of Venus flytrap (*Dionaea muscipula* Ellis). *Planta* 179(1): 32–42.

Horstmann M, Heier L, Kruppert S et al. (2019) Comparative prey spectra analyses on the endangered aquatic carnivorous waterwheel plant (*Aldrovanda vesiculosa*, Droseraceae) at several naturalized microsites in the Czech Republic and Germany. *Integrative Organismal Biology* 1(1): oby012.

Ionov L (2014) Hydrogel-based actuators: Possibilities and limitations. *Materials Today* 17(10): 494–503.

Kim SW, Ko JS, Lee JG et al. (2014) Flytrap-inspired robot using structurally integrated actuation based on bistability and a developable surface. *Bioinspiration & Biomimetics* 9(3): 36004.

Knippers J, Scheible F, Oppe M et al. (2012) Bio-inspired kinetic GFRP- façade for the thematic pavilion of the EXPO 2012 in Yeosu. In: *International Symposium of Shell and Spatial Structures (IASS 2012), Yeosu, South Korea*, pp.341–347. Madrid: International Association for Shell and Spatial Structures.

Knippers J, Schmid U and Speck T (eds.) (2019) *Biomimetics for Architecture. Learning From Nature*. Basel: Birkhäuser Verlag.

Kohlmeyer RR and Chen J (2013) Wavelength-selective, IR light-driven hinges based on liquid crystalline elastomer composites. *Angewandte Chemie (International ed. in English)* 52(35): 9234–9237.

Körner A, Born L, Mader A et al. (2018) Flectofold—A biomimetic compliant shading device for complex free form façades. *Smart Materials and Structures* 27(1): 017001.

Kronestedt E and Walles B (1986) Anatomy of the *Strelitzia reginae* flower (Strelitziaceae). *Nordic Journal of Botany* 6(3): 307–320.
Laschi C, Rossiter J, Iida F et al. (eds.) (2017) Soft Robotics: Trends, Applications and Challenges. Cham: Springer International Publishing.

Le Duigou A and Castro M (2016) Evaluation of force generation mechanisms in natural, passive hydraulic actuators. Scientific Reports 6: 18105.

Lee H, Xia C and Fang NX (2010) First jump of microgel; actuation speed enhancement by elastic instability. Soft Matter 6(18): 4342.

Lienhard J, Schleicher S, Poppinga S et al. (2011) Flectofin: A hingeless flapping mechanism inspired by nature. Bioinspiration & Biomimetics 6(4): 045001.

Lim H, Park T, Na J et al. (2017) Construction of a photothermal Venus flytrap from conductive polymer bimorphs. NPG Asia Materials 9(7): e399.

MacKinnon RB, Oomen J and Pedersen Zari M (2020) Promises and presuppositions of biomimicry. Biomimetics 5(3): 33.

Mader A, Birkhold A, Caliaro M et al. (2017) Plant-inspired compliant actuation. In: Proceedings of the 7th GACM Colloquium on Computational Mechanics for Young Scientists from Academia and Industry, pp.233–237. Stuttgart: Institute for Structural Mechanics, University of Stuttgart.

Mader A, Langer M, Knippers J et al. (2020) Learning from plant movements triggered by bulliform cells: The biomimetic cellular actuator. Journal of the Royal Society Interface 17(169): 0200358.

Majidi C (2018) Soft-matter engineering for soft robotics. Advanced Materials Technologies 4(2): 1800477.

Markin VS, Volkov AG and Jovanov E (2008) Active movements in plants. Plant Signaling & Behavior 3(10): 778–783.

Masselter T, Bold G, Thielen M et al. (2018) Bio-inspired materials and structures: A case study based on selected examples. In: Yang G, Xiao L and Lamboni L (eds.) Bioinspired Materials Science and Engineering. pp.253–266. Hoboken, NJ: John Wiley & Sons.

Mazzolai B, Mondini A, Del Dottore E et al. (2020a) Self-growing adaptable soft robots. In: Koshima H (ed.) Mechanically Responsive Materials for Soft Robotics. pp.363–394. Weinheim, Germany: Wiley-VCH.

Mazzolai B, Walker I and Speck T (eds.) (2020b) Research topic on generation GrowBots: Materials, mechanisms, and biomimetic design for growing robots. Frontiers of Robotics and AI 8: 711942.

Meder F, Thielen M, Mondini A et al. (2020) Living plant-based generators for multidirectional wind energy conversion. Energy Technology 2020: 2000236.

Must I, Sinibaldi E and Mazzolai B (2019) A variable-stiffness tendril-like soft robot based on reversible osmotic actuation. Nature Communications 10(1): 344.

Pal A, Goswami D and Martinez RV (2020) Elastic energy storage enables rapid and programmable actuation in soft machines. Advanced Functional Materials 30(1): 1906603.

Poppinga S, Bauer U, Speck T et al. (2018a) Motile traps. In: Ellison AM and Adamec L (eds.) Carnivorous Plants: Physiology, Ecology, and Evolution. Oxford: Oxford University Press, pp.180–193.

Poppinga S, Correa D, Bruchmann B et al. (2020) Plant movements as concept generators for the development of biomimetic compliant mechanisms. Integrative and Comparative Biology 60(4): 886–895.

Poppinga S and Joyeux M (2011) Different mechanisms of snap-trapping in the two closely related carnivorous plants Dionaea muscipula and Aldrovanda vesiculosa. Physical Review E 84: 041928.

Poppinga S, Kampowski T, Metzger A et al. (2016) Comparative kinamtical analyses of Venus flytrap (Dionaea muscipula) snap-traps. Beilstein Journal of Nanotechnology 7: 664–674.

Poppinga S, Lienhard J, Schleicher S et al. (2010) Ge-kenkreie Klappen bei Strelitzia reginae. In: Kesel AB and Zehren D (eds.) Bionik: Patente aus der Natur. Tagungsbeiträge zum 5. Bionik-Kongress. Bremen: Hochschule Bremen, pp.320–326.

Poppinga S, Masselter T and Speck T (2013) Faster than their prey: New insights into the rapid movements of active carnivorous plants traps. BioEssays 35(7): 649–657.

Poppinga S, Nestle N, Šandor A et al. (2017) Hygroscopic motions of fossil conifer cones. Scientific Reports 7: 40302.

Poppinga S, Smajl J, Westermeier AS et al. (2019) Prey capture analyses in the carnivorous aquatic water-wheel plant (Aldrovanda vesiculosa L., Droseraceae). Scientific Reports 9: 18590.

Poppinga S, Zollfrank C, Prucker O et al. (2018b) Toward a new generation of smart biomimetic actuators for architecture. Advanced Materials 30(19): 1703653.
Reyssat E and Mahadevan L (2009) Hygromorphs: From pine cones to biomimetic bilayers. *Journal of the Royal Society Interface* 6(39): 951–957.

Riley KS, Ang KJ, Martin KA et al. (2020) Encoding multiple permanent shapes in 3D printed structures. *Materials & Design* 194: 108888.

Ritzmann RE, Quinn RD and Fischer MS (2004) Convergent evolution and locomotion through complex terrain by insects, vertebrates and robots. *Arthropod Structure & Development* 33(3): 361–379.

Rowan MK (1974) Bird pollination of *Strelitzia*. *Ostrich* 45: 40.

Sachse R, Westermeier A, Mylo M et al. (2020) Snapping mechanics of the Venus flytrap (*Dionaea muscipula*). *Proceedings of the National Academy of Sciences of the United States of America (PNAS)* 117(27): 16035–16042.

Sadeghi A, Del Dottore E, Mondini A et al. (2020) Passive morphological adaptation for obstacle avoidance in a self-growing robot produced by additive manufacturing. *Soft Robotics* 7(1): 85–94.

Saffarian S, Born L, Körner A et al. (2019) From pure research to biomimetic products: The Flectofold facade shading device. In: Knippers J, Schmid U and Speck T (eds.) *Biomimetics for Architecture: Learning from Nature*. Basel: Birkhäuser Verlag, pp.42–51.

Schleicher S, Lienhard J, Poppinga S et al. (2015) A methodology for transferring principles of plant movements to elastic systems in architecture. *Computer-Aided Design* 60: 105–117.

Schmied JU, Le Ferrand H, Ermanni P et al. (2017) Programmable snapping composites with bio-inspired architecture. *Bioinspiration & Biomimetics* 12(2): 26012.

Sequeira AA, Usman A, Tharakan OP et al. (2016) Biologically inspired robots in a new dimension – A review. *International Journal of Automation, Mechatronics & Robotics* 3(1): 106–116.

Skotheim JM and Mahadevan L (2005) The Venus flytrap as a model for a biomimetic material with built-in sensors and actuators. *Materials Science and Engineering: C* 2(4): 229–233.

Shahinpoor M and Thompson MS (1995) The Venus flytrap as a model for a biomimetic material with built-in metal composites. *Bioinspiration & Biomimetics* 6(4): 46004.

Skead CJ (1975) Weaverbird pollination of *Strelitzia reginae*. *Ostrich* 46: 183–185.

Speck T (2015) Approaches to bio-inspiration in novel architecture. In: Imhof B and Gruber P (eds.) *Built to Grow – Blending Architecture and Biology*. Basel: Birkhäuser Verlag, pp.145–149.

Speck T (2019) Roadmap on soft robotics ‘Materials inspired by plants’. *Multifunctional Materials* (under review).

Speck T and Speck O (2008) Process sequences in biomimetic research. In: Brebbia CA (ed.) *Design and Nature IV*. Southampton: WIT Press, pp.3–11.

Speck T and Speck O (2019a) Emergence in biomimetic materials systems. In: Wegner L and Lütge U (eds.) *Emergence and Modularity in Life Sciences*. Cham: Springer, pp.97–115.

Speck T and Speck O (2019b) Quo vadis plant biomechanics – Old wine in new bottles or an up-and-coming field of modern plant science? *American Journal of Botany* 106(11): 1–5.

Speck T and Speck O (2017) Biomimetic bio-inspired biomorph sustainable? An attempt to classify and clarify biology-derived technical developments. *Bioinspiration & Biomimetics* 12(1): 011004.

Speck O, Speck D, Horn R et al. (2017) Biomimetic bio-inspired biomorph sustainable? An attempt to classify and clarify biology-derived technical developments. *Bioinspiration & Biomimetics* 12(1): 011004.

Steffen W, Grinevald J, Crutzen P et al. (2011) The Anthropocene: Conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 369(1938): 842–867.

Suda H, Mano H, Toyota M et al. (2020) Calcium dynamics during trap closure visualized in transgenic Venus flytrap. *Nature Plants* 6: 1219–1224.

Suda H, Mano H, Toyota M et al. (2020) Calcium dynamics during trap closure visualized in transgenic Venus flytrap. *Nature Plants* 6: 1219–1224.

Tedeshi F and Carbone G (2014) Design issues for hexapod walking robots. *Robotics* 3(2): 181–206.
Temirel M, Yenilmez B, Knowlton S et al. (2016) Three-dimensional-printed carnivorous plant with snap trap. *3D Printing and Additive Manufacturing* 3(4): 244–251.

Timoshenko S (1925) Analysis of bi-metal thermostats. *Journal of the Optical Society of America* 11(3): 233–255.

Trahair N (1993) *Flexural–Torsional Buckling of Structures*. Boca Raton, FL: CRC Press.

van de Kamp T, Vagović P, Baumbach T et al. (2011) A biological screw in a beetle’s leg. *Science* 333(6038): 52.

Vincent JFV (2002) Survival of the cheapest. *Materials Today* 5(12): 28–41.

Virtual Exhibition Tour – Exhibition “Baubionik – Biologie beflügelt Architektur” in the Museum for Natural History in Stuttgart (19th October 2017 to 6th May 2018). Available at: https://www.trr141.de/180409_Bionik/ (accessed 22 October 2020).

Volkov AG, Forde-Tuckett V, Volkova M et al. (2014) Morphing structures of the *Dionaea muscipula* Ellis during the trap opening and closing. *Plant Signaling & Behavior* 9(2): e27793.

Wang X, Khara A and Chen C (2020) A soft pneumatic bistable reinforced actuator bioinspired by Venus flytrap with enhanced grasping capability. *Bioinspiration & Biomimetics* 15(5): 056017.

Wani OM, Zeng H and Priimagi A (2017) A light-driven artificial flytrap. *Nature Communications* 8: 15546.

Westermeier AS, Hiss N, Speck T et al. (2020) Functional-morphological analyses of the delicate snap-traps of the aquatic carnivorous waterwheel plant (*Aldrovanda vesiculosa*) with 2D and 3D imaging techniques. *Annals of Botany* 126: 1099–1107.

Westermeier AS, Poppinga S, Körner A et al. (2019) No joint ailments: How plants move and inspire technology. In: Knippers J, Schmid U and Speck T (eds.) *Biomimetics for Architecture: Learning from Nature*. Basel: Birkhäuser Verlag, pp.32–41.

Westermeier AS, Sachse R, Poppinga S et al. (2018) How the carnivorous waterwheel plant (*Aldrovanda vesiculosa*) snaps. *Proceedings of the Royal Society B: Biological Sciences* 285(1878): 20180012.

Yang R, Lenaghan SC, Li Y et al. (2012) Mathematical modeling, dynamics analysis and control of carnivorous plants. In: Volkov AG (ed.) *Signaling and Responses*. Heidelberg: Springer, pp.63–83.

Zhang Z, Chen D, Wu H et al. (2016) Non-contact magnetic driving bioinspired Venus flytrap robot based on bistable anti-symmetric CFRP structure. *Composite Structures* 135: 17–22.

Zhu Y, Zhang J, Wu Q et al. (2020) Three-dimensional programmable, reconfigurable, and recyclable biomass soft actuators enabled by designing an inverse opalmimetic structure with exchangeable interfacial crosslinks. *ACS Applied Materials & Interfaces* 12(13): 15757–15764.