

CORRECTION

Correction: Passive water collection with the integument: mechanisms and their biomimetic potential (doi:10.1242/jeb.153130)

Philipp Comanns

There was an error published in *J. Exp. Biol.* (2018) **221**, jeb153130 (doi:10.1242/jeb.153130).

The corresponding author's email address was incorrect. It should be Philipp.Comanns@rwth-aachen.de. This has been corrected in the online full-text and PDF versions.

We apologise to authors and readers for any inconvenience this may have caused.

REVIEW

Passive water collection with the integument: mechanisms and their biomimetic potential

Philipp Comanns*

ABSTRACT

Several mechanisms of water acquisition have evolved in animals living in arid habitats to cope with limited water supply. They enable access to water sources such as rain, dew, thermally facilitated condensation on the skin, fog, or moisture from a damp substrate. This Review describes how a significant number of animals – in excess of 39 species from 24 genera – have acquired the ability to passively collect water with their integument. This ability results from chemical and structural properties of the integument, which, in each species, facilitate one or more of six basic mechanisms: increased surface wettability, increased spreading area, transport of water over relatively large distances, accumulation and storage of collected water, condensation, and utilization of gravity. Details are described for each basic mechanism. The potential for bio-inspired improvement of technical applications has been demonstrated in many cases, in particular for several wetting phenomena, fog collection and passive, directional transport of liquids. Also considered here are potential applications in the fields of water supply, lubrication, heat exchangers, microfluidics and hygiene products. These present opportunities for innovations, not only in product functionality, but also for fabrication processes, where resources and environmental impact can be reduced.

KEY WORDS: Water collection, Moisture harvesting, Biomimetic, Capillary channel, Surface structures, Hydrophilic, Wetting

Introduction

There are numerous studies investigating the adaptations in nature to limited resources. Some reptiles, amphibians, arthropods, birds and even mammals have been found to survive restrictions on water supply by using their body surface to collect water from various sources (Louw, 1972; Rijke, 1972; Lillywhite and Licht, 1974; Gans et al., 1982; Lillywhite and Stein, 1987; Sherbrooke, 1990; Cardwell, 2006; Tracy et al., 2011). Collecting water in arid environments might appear to be contradictory at first, but nevertheless many such areas are known to provide water sources. For example, dew is regularly found in most deserts early in the morning, originating from significant day–night temperature differences (Louw, 1972). The Namib desert is famous for its fog (Shanyengana et al., 2002); depending on the location, fog events occur 40–200 days per year (Seely, 1979; Shanyengana et al.,

2002). Furthermore, there are also infrequent rain falls that must be considered (Comanns et al., 2016a).

Maintaining a water balance in xeric habitats (see Glossary) often requires significant reduction of cutaneous water loss. Reptiles commonly have an almost water-proof skin owing to integumental lipids, amongst other components (Hadley, 1989). In some snakes, for example, the chemical removal of lipids has been shown to increase transepidermal water permeation by a factor of 35–175 (Burken et al., 1985).

Amphibians, by contrast, typically lack a significant resistance to cutaneous water loss (Bentley and Schmidt-Nielsen, 1966; Shoemaker and Nagy, 1977; Toledo and Jared, 1993; Maderson et al., 1998; Lillywhite, 2006). The low resistance to cutaneous water loss can be seen as a cost for transcutaneous water uptake and respiration requiring a moist skin (Chew, 1961). In some arboreal hyliid frogs, however, a significant reduction of evaporative water loss is provided by a cutaneous secretion of lipids (Shoemaker et al., 1972; Blaylock et al., 1976; McClanahan et al., 1978; Toledo and Jared, 1993; Amey and Grigg, 1995; Tracy et al., 2011). Similarly, arthropods achieve reduced water loss by protective lipid and wax layers of the cuticle (Beament, 1964; Edney, 1977; Hadley, 1989, 1991).

Despite such reduction of water loss, additional water demand has been found in many species. In desert reptiles, a number of species require additional water collection, although they often rely to a large degree on the water content of their diet to cover their water demand (Bentley and Blumer, 1962; Nagy, 1987; Maderson et al., 1998; Lillywhite, 2006). For some desert lizards, this necessity results from their mainly myrmecophagous diet (see Glossary), which demands special mechanisms to support excretion of high concentrations of electrolytes (Bradshaw and Shoemaker, 1967; Withers and Dickman, 1995). Lately, some studies on diet-based water demand discuss the uptake of free water as a general strategy for a number of desert reptiles, in particular carnivorous reptiles, which often show a more or less distinct need for uptake of free water in order to obtain a net gain of water (Wright et al., 2013; Lillywhite, 2017). In many amphibians, water collection is required to replenish the water loss from mucus secretion, in particular for thermoregulation and counteracting dehydration of the epidermis (see Glossary) at higher temperatures (Lillywhite and Licht, 1975; Lillywhite et al., 1998). Some toads prevent dehydration of the skin directly by collecting water from their environment (Lillywhite and Licht, 1974). In general, the need for water collection is often for rehydration, but it is also needed for water adsorption, which prevents dehydration of the skin (Lillywhite and Licht, 1974). Furthermore, collected water serves the thermoregulation in elephants and wharf roaches (Hoese, 1981; Lillywhite and Stein, 1987), is transported by adult sandgrouse from water sources to hydrate the young (Cade and MacLean, 1967), and yields reduced reflectivity for camouflage in flat bugs (Silberglied and Aiello, 1980; Hischen et al., 2017).

Passive water collection takes place from sources of the animals' environment; for example, from water puddles, infrequent

RWTH Aachen University, Institute of Biology II (Zoology), Worringerweg 3, 52074 Aachen, Germany.

*Author for correspondence (Philipp.Comanns@rwth-aachen.de)

 P.C., 0000-0002-2020-0515

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Glossary**Condensation**

Phase transition of water from gaseous to liquid.

Contact angle

Quantification of the liquid–substrate interaction (see Fig. 2).

Epidermis

The outer skin layers.

Hydrophilic substrate

A substrate that can be wetted by aqueous liquids.

Hydrophobic substrate

Water-repellent substrate surface.

Hygroscopic substrate

A material that can absorb moisture from air.

Integument

Body surface of animals (skin or cuticle), including its derivatives such as scales, feathers, etc.

Laser ablation

Removal (often favoured: sublimation) of substrate material by laser irradiation.

Micromilling

A rotating cutting fabrication method in the micrometre range.

Myrmecophagous diet

A diet mostly consisting of ants.

Oleophilic substrate

A substrate that can be wetted by oil.

Pennaceous feather

A type of feather present in most modern birds: containing a quill/rachis with barbs at either side that are linked to each other by barbules to form the vanes.

Pinning

Holding of a liquid front in micrometre ranges.

Spreading

Distribution of a liquid on a substrate surface.

Wettability

Interaction of a liquid and substrate surface, typically quantified by contact angle (see Fig. 2).

Xeric habitat

Dry environment.

precipitation, moist substrate, air humidity and dew or fog (Table 1). In cases of water collection from infrequent precipitation or fog, a number of species, such as snakes (Louw, 1972; Robinson and Hughes, 1978; Andrade and Abe, 2000; Cardwell, 2006; Repp and Schuett, 2008; Glaudas, 2009), tortoises (Auffenberg, 1963), lizards (Schwenk and Greene, 1987; Sherbrooke, 1990; Veselý and Modrý, 2002) and beetles (Hamilton and Seely, 1976; Nørgaard and Dacke, 2010), expose themselves to the water source by using a stereotypic behaviour (Table 1), while the actual water collection remains passive (Joel et al., 2017).

In this Review, I focus on mechanisms to passively collect water with the integument (see Glossary) of animals. As the collection and handling of water has also been of particular interest regarding their potential for nature-inspired improvement of technical applications, a comprehensive overview of analyzed animal species can catalyze further studies and innovations. Several water-collection mechanisms have been adapted for technical applications using a biomimetic approach, and examples are subsequently discussed.

Basic mechanisms for water collection

The ability to passively collect water with the body surface can be found in a broad variety of genera. Mechanisms have evolved to access various sources, such as rain, fog, water vapour in air and moisture from the animal's surrounding substrate. The collection of water is followed by a transcutaneous uptake (amphibians), direct

drinking (snakes), spreading (see Glossary) over the body surface (toads, elephants, flat bugs and beetles), transport to other parts of the body surface (lizards, tortoises and wharf roaches) or storage in the plumage (sandgrouse) (Table 1). In the end, water is incorporated in some way in all described cases, but not in flat bugs and elephants.

These collection processes and subsequent handling of collected water involve different, specific chemical or structural adaptations of the body surface. Based on these general considerations, six basic mechanisms have been identified as being involved in passive water collection (Fig. 1): (1) increased surface wettability; (2) increased spreading area; (3) transport of water over relatively large distances; (4) accumulation and storage of collected water; (5) facilitating condensation; and (6) utilization of gravity (see Glossary for the terms described).

In more detail, an increased surface wettability of the integument (1), i.e. smaller contact angles (see Glossary), results from either chemical properties and/or microstructures (Fig. 2), such as different kinds of pillar and hexagonal dimples (Bormashenko, 2010; Comanns et al., 2014). The spreading area (2) can be increased by similar microstructures, which allow subsequent drinking of water (Bico et al., 2002; Chandra and Yang, 2011). Further structures, i.e. grooves or channels, are required to transport water (3) over larger distances or precisely in one direction (Berthier and Silberzan, 2010; Comanns et al., 2015). It is important to note the difference between wetting effects and capillarity. The former is the interaction of liquids with (structured) surfaces, whereas the latter is the force acting on the liquid within channel structures (Berthier and Silberzan, 2010). In the examples given in Table 1, transportation distances are typically in the range of few millimetres to several centimetres. Besides these structure-based mechanisms to collect and/or transport water, hairy surface appendages such as feathers facilitate a mechanism for passive accumulation and storage of water (4) (Joubert and MacLean, 1973). Condensation (5) is facilitated by changing the microhabitat to establish a thermal gradient to ambient conditions, i.e. making the body cooler than the surrounding (Tracy et al., 2011). And finally, there are several instances of gravity (6) being utilized by adopting a particular body posture to channel the water to the mouth for drinking (Auffenberg, 1963). In some cases, combinations of these basic mechanisms are found.

Surface wettability

The ability to passively collect water with the integument appears to require hydrophilic surfaces (see Glossary), independent of species (Table 1). Hydrophilicity means an increased wettability of the integument, which results from chemical properties and often exists in combination with certain microstructures (Box 1).

In desert lizards, a number of species within the genera *Phrynosoma*, *Phrynocephalus*, *Trapelus*, *Moloch*, *Pogona*, *Cordylus* and *Uromastix* are known to passively collect water from their environment (Ditmars, 1933; Pianka and Pianka, 1970; Gans et al., 1982; Fitzgerald, 1983; Schwenk and Greene, 1987; Sherbrooke, 1990, 1993, 2004; Withers, 1993; Peterson, 1998; Veselý and Modrý, 2002; Yenmiş et al., 2015). To rationalize the nomenclature for the different sources of water acquisition, they have been termed 'moisture-harvesting lizards' (Comanns et al., 2011). The keratinous skin of these moisture-harvesting lizards is hydrophilic and exhibits hexagonal microstructures on the scale surfaces (Fig. 1A) (Comanns et al., 2011). Typical dimensions of these structures are diameters of 10–30 µm and depths of 1–5 µm (Comanns et al., 2011). Once in contact with tiny amounts of water, the microstructures get filled with water and render the skin surface

Table 1. Passive integumental water collection in animals

Animal class	Species	Water source	Collection mechanism	Surface structures or chemistry	Further handling and function	References
Amphibians (tree frogs)	<i>Phyllomedusa sauvagii</i>	Humidity	Condensation on skin	Hygroscopic secretion, slightly granular skin	Transcutaneous uptake	Shoemaker et al., 1972; Toledo and Jared, 1993
	<i>Litoria caerulea</i>					Toledo and Jared, 1993; Tracy et al., 2011
Amphibians (toads)	<i>Anaxyrus boreas</i>	Moist substrate	Skin-wetting properties, capillarity	Ridges, channels	Skin wetting and capillary transport to replenish evaporative loss	Fair, 1970; Lillywhite and Licht, 1974; Toledo and Jared, 1993
	<i>Anaxyrus woodhousii</i>					Lillywhite and Licht, 1974
	<i>Anaxyrus punctatus</i>					McClanahan and Baldwin, 1969; Fair, 1970
Reptiles (tortoises)	<i>Psammobates tentorius trimeni</i> * <i>Kinixys homeana</i> * <i>Homopus areolatus</i> *	Rain	Exposure of body surface to rain, utilizing gravity	Large ridges of carapace	Gravity-facilitated transport on surface to mouth for drinking	Auffenberg, 1963 Auffenberg, 1963 Auffenberg, 1963
Reptiles (lizards)	<i>Phrynosoma cornutum</i> *	Moist substrate, rain	Skin-wetting properties, capillarity	Honeycomb-like microstructure, channels between the scales	Transport in channels between scales from all body parts to mouth for drinking	Sherbrooke, 1990; Sherbrooke, 2004; Sherbrooke et al., 2007
	<i>Phrynosoma modestum</i> *					Sherbrooke, 2002
	<i>Phrynosoma platyrhinos</i> *					Planka and Parker, 1975; Peterson, 1998
	<i>Phrynoscephalus arabicus</i>					Comanns et al., 2011
	<i>Phrynoscephalus helioscopus</i> *					Schwenk and Greene, 1987
	<i>Phrynoscephalus horvathi</i> *					Yenmiş et al., 2015
	<i>Trapelus flavimaculatus</i> *					Vesely and Modry, 2002
	<i>Trapelus pallidus</i> *					Vesely and Modry, 2002
	<i>Trapelus mutabilis</i> *					Vesely and Modry, 2002
	<i>Moloch horridus</i>					Bentley and Blumer, 1962; Gans et al., 1982; Sherbrooke, 1993; Withers, 1993; Sherbrooke et al., 2007
Reptiles (snakes)	<i>Uromastix spinipes</i>	Rain		Channels between the scales n.d. n.d.	Direct drinking of collected water	Ditmars, 1933 Fitzgerald, 1983 Louw, 1972
	<i>Pogona vitticeps</i> *	Fog	Fog basking			
	<i>Aporosaura anchietae</i>					
	<i>Crotalus atrox</i> *	Rain	Accumulation of collected water	n.d.	Drinking from body surface	Repp and Schuett, 2008
	<i>Crotalus mitchellii pyrrhus</i> * <i>Crotalus viridis concolor</i> * <i>Crotalus s. scutulatus</i> * <i>Bothrops moojeni</i> * <i>Bitis peringueyi</i> *	Rain, fog				Glaudas, 2009 Ashton and Johnson, 1998 Cardwell, 2006 Andrade and Abe, 2000 Louw, 1972; Robinson and Hughes, 1978
Mammals (elephants)	<i>Acrochordus granulatus</i>	Open water, wet substrate	Skin-wetting properties, capillarity	Hygroscopic skin, capillary channels	Prevent dehydration	Lillywhite and Sanmartino, 1993
	<i>Loxodonta africana</i> <i>Elephas maximus</i>	Open water/lakes	Skin-wetting properties, capillarity	Ridges/grooves	Thermoregulation, reduction of dehydration	Lillywhite and Stein, 1987 Lillywhite and Stein, 1987
	<i>Pterocles bicinctus</i> <i>Pterocles namaqua</i>	Open water/lakes	Capillarity	Hairy feather structure	Storage between feathers, direct drinking by chicks	Cade and MacLean, 1967 Joubert and MacLean, 1973

Continued

Table 1. Continued

Animal class	Species	Water source	Collection mechanism	Surface structures or chemistry	Further handling and function	References
Insects (beetles)	<i>Onymacris unguicularis</i> *	Fog	Fog basking	Patchwork of hydrophilic and hydrophobic parts	Wetting properties of elytra, gravity	Hamilton and Seely, 1976; Seely, 1979; Nørgaard and Dacke, 2010
	<i>Onymacris bicolor</i> *					Seely, 1979; Nørgaard and Dacke, 2010
	<i>Stenocara</i> sp.					Parker and Lawrence, 2001
Insects (flat bugs)	<i>Dysodius lunatus</i>	Rain	Hydrophilic cuticle, capillarity	Hydrophilic waxes, spine microstructures, channels	Reducing reflectivity, aiding camouflage	Hischen et al., 2017
	<i>Dysodius magnus</i>					Hischen et al., 2017
Crustacea (wharf roaches)	<i>Ligia exotica</i> <i>Ligia oceanica</i>	Moist substrate	Hydrophilic cuticle, capillarity	Channels between hair-like and paddle-like protrusions	Thermoregulation or transport to hindgut for uptake	Horiguchi et al., 2007; Ishii et al., 2013 Hoesle, 1981

*Stereotypic behaviour. n.d., not determined.

Box 1. Influence of surface roughness on wetting properties

Wetting describes a liquid–solid interaction commonly quantified by the contact angle, which is specific for each liquid–solid combination (Fig. 2) (Quéré, 2008; Spori et al., 2008). The contact angle can be calculated by the Young equation for chemically homogeneous, ideally flat surfaces at equilibrium according to the underlying interfacial energies (Butt et al., 2003; de Gennes et al., 2003). Chemically heterogeneous surfaces, such as the covering wings (elytra) from darkling beetles in the Namib desert (Parker and Lawrence, 2001; Nørgaard and Dacke, 2010) can be described by the model from Cassie and Baxter (Cassie and Baxter, 1944). By taking into consideration additional roughness or nano-/micrometre-level surface structures, wetting properties can be further modified, as modelled by Wenzel (wetting on rough surfaces; Wenzel, 1936) or Cassie and Baxter (entrapping of air; Cassie and Baxter, 1944). For wetting states modelled by Wenzel, one can observe the tendency that roughness increases the hydrophilicity or hydrophobicity compared with ideally flat surfaces (Quéré, 2008). Such increase of chemical wetting properties by surface roughness is even required for some ranges of contact angles, in particular smaller than about 10 deg and larger than about 120 deg (Fig. 2) (Extrand, 2002; Quéré, 2008; Spori et al., 2008). Besides random roughness, specific geometric roughness in the range of nanometres and micrometres can also be used to control the wetting behaviour of a specific liquid–material combination (Zu et al., 2010; Kumar and Errington, 2013). The more precisely that a material surface can be manufactured, the more specific the modification of its wetting properties. In general, surface modifications can be either chemical (Dorner and Rühle, 2008b; Domachuk et al., 2010; Ghosh et al., 2014) and/or structural (Koch and Barthlott, 2009; Barthlott et al., 2010; Hancock et al., 2012), and either improve or decrease the surface wettability.

‘superhydrophilic’ (Fig. 3) (Comanns et al., 2016a). Such water-filling has been considered as pre-wetting, which is likely a preparation for faster uptake of water from more-efficient sources, such as damp sand (Comanns et al., 2016a).

Chemical modifications of the integument are found in secretions of hylid frogs (Toledo and Jared, 1993; Tracy et al., 2011) or ‘hydrophilizing’ components in waxes of flat bugs (Hischen et al., 2017). Some arboreal hylid frogs, such as *Phyllomedusa sauvagii* or *Litoria caerulea*, significantly reduce evaporative water loss by a cutaneous secretion of lipids (Shoemaker et al., 1972; Blaylock et al., 1976; McClanahan et al., 1978; Toledo and Jared, 1993; Amey and Grigg, 1995; Tracy et al., 2011). After secretion, the secreted fluid is spread over the body surface by wiping behaviour to obtain a protective coating (Toledo and Jared, 1993; Barbeau and Lillywhite, 2005). The lipid secretions have been considered as having hygroscopic (see Glossary) properties and resulting in a wettable skin surface (Toledo and Jared, 1993). Some toads modify their skin-wetting properties in a comparable way. For example, in their parotoid glands, *Anaxyrus* sp. toads produce a venomous secretion. Although this secretion primarily serves as defensive liquid, it contains *inter alia* glycosaminoglycans, which are hygroscopic substances that again are considered to play a role in water balance (Toledo et al., 1992). In contrast, many sun-basking species, such as the American bullfrog *Rana catesbeiana*, appear to use mucus secretions for maintaining the water balance of the epidermis rather than for (direct) collection of water (Lillywhite and Licht, 1975).

The South American flat bug species *Dysodius lunatus* and *Dysodius magnus* collect water for camouflage, in which they reduce their surface reflectivity, rather than rehydration (Silberglied and Aiello, 1980; Reischwich, 2013; Hischen et al., 2017). Immediate spreading of water droplets is facilitated by chemical and structural

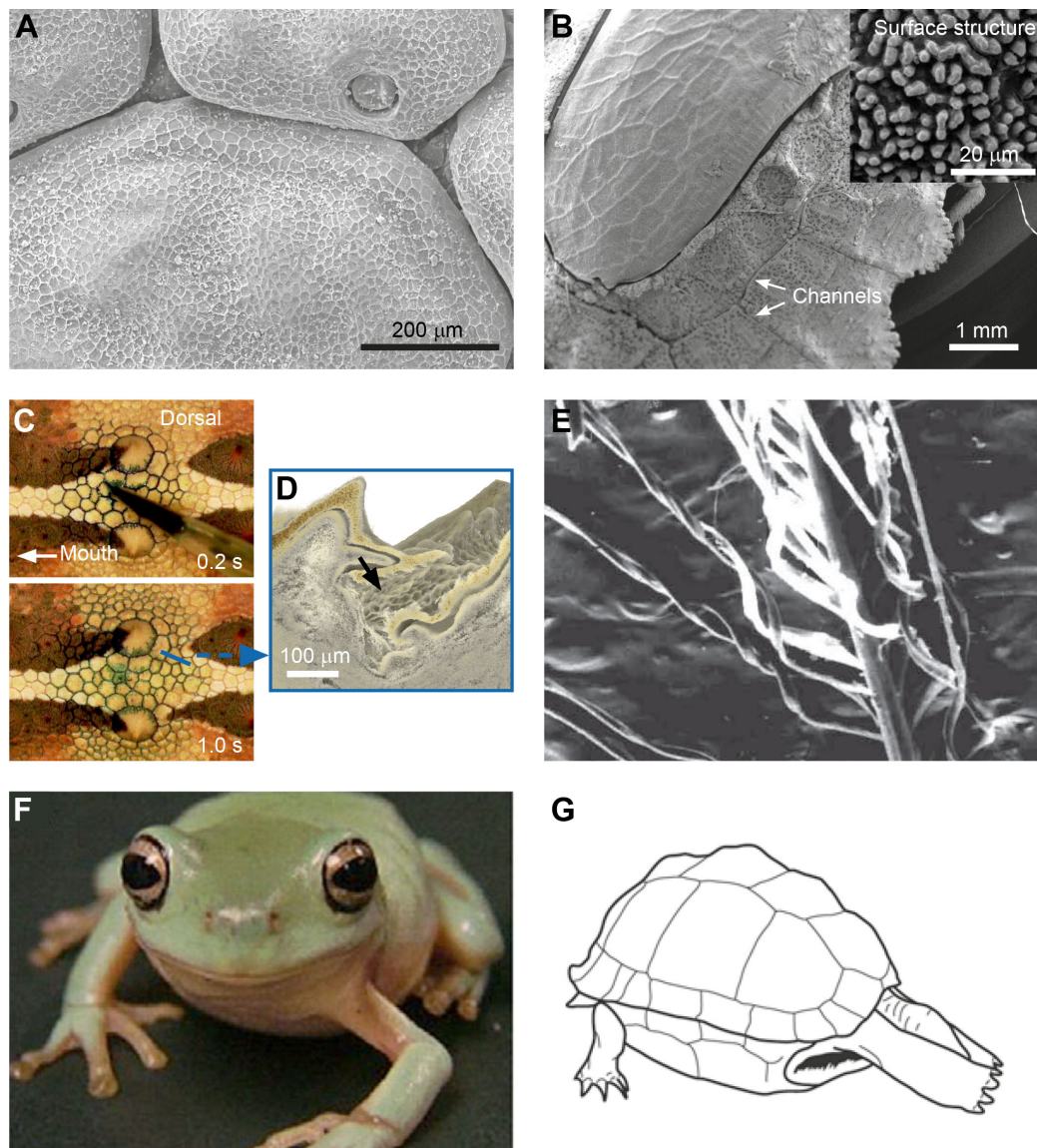


Fig. 1. Examples of integument surface structures and their resulting wetting properties. (A) Hexagonal microstructure on the dorsal scales of the horned lizard *Phrynosoma platyrhinos*. The surface wettability increases when a water film is held by pre-wetting (modified from Hermens et al., 2017, ©2017, with permission from Elsevier). (B) Increased spreading area by pillar-like surface structures of the flat bug *Dysodius magnus* (adapted from Hischen et al., 2017, with permission from Biology Open 2017). (C) Transport of dyed water within skin channel structures of the Australian thorny devil, *Moloch horridus* (reproduced from Comanns et al., 2017, licensed under CC-BY 4.0). (D) Cross-section through the skin using microcomputed tomography (µCT) (exemplary position is indicated in C). The black arrow indicates the channel cavity. (Reproduced from Comanns et al., 2017, licensed under CC-BY 4.0). (E) Storage of collected water by means of the breast feather structures of, for example, the sandgrouse *Pterocles namaqua* (438×; reproduced from Joubert and MacLean, 1973, *Zoologica Africana* 8, 141-152 with permission ©NISC Pty Ltd). (F) Facilitating condensation by means of skin structure in conjunction with an advantageous temperature gradient of tree frog *Litoria caerulea* (reproduced with permission from Scholz et al., 2009). (G) Utilization of gravity by body elevation for directing captured water flow in tortoises: illustrated here is the tent tortoise *Psammobates tentorius trimeni* [from Joel et al., 2017, reprinted with permission from Springer: Springer Nature, *Functional Surfaces in Biology III* by S. Gorb and E. Gorb (ed.), ©2017].

properties of the integument. Unlike most other insects, the cuticle of these bugs is covered by a hydrophilic wax layer imparted by the amphiphilic component erucamide (Hischen et al., 2017).

Microstructures to create water penetration

Surface structures do not only affect the surface wetting properties in terms of contact angle, but wetting phenomena in general. Wetting phenomena include, for example, water repellence and self-cleaning (Barthlott and Neinhuis, 1997), pinning (see Glossary) of the advancing water front at surface microstructures (Bico et al., 2002; Lai et al., 2012; Srinivasan et al., 2014) or penetration into the

structured surface area (Bico et al., 2002; Chandra and Yang, 2011). Water penetration into surface structures with moderate chemical hydrophilicity can cover greater areas than are possible by spreading on a smooth surface (Quéré, 2008). Such water penetration has been found, for example, in toads (Lillywhite and Licht, 1974), elephants (Lillywhite and Stein, 1987) and flat bugs (Hischen et al., 2017).

Some hyliid toads of the genus *Anaxyrus* (e.g. *A. boreas*, *A. woodhousii*, *A. punctatus*) collect water from moist substrates (McClanahan and Baldwin, 1969; Fair, 1970; Lillywhite and Licht, 1974; Toledo and Jared, 1993). Their granular skin contains numerous grooves in which capillary forces occur that suck water

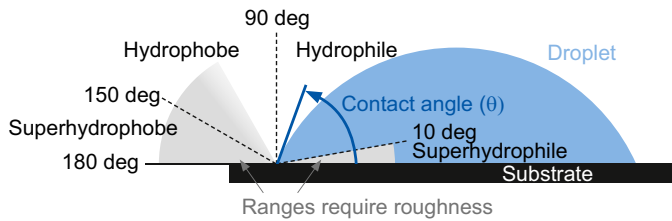


Fig. 2. Contact angle as quantification of wetting properties. The contact angle (θ) is commonly measured for sessile droplets at the contact point of droplet surface and substrate in the horizontal perspective. It is defined as the angle between the tangent of the droplet and the substrate surface. The given ranges are obtained from Extrand (2002), Quéré (2008), Spori et al. (2008) and Koch et al. (2009). For an explanation of surface wetting properties, see also Box 1.

from the substrate. Accumulated water is transported even to the dorsal body parts, most likely to maximize effective wetting of the skin to enlarge the area for water uptake (amphibians typically absorb water through the skin) and to prevent dehydration of the epidermis (Lillywhite and Licht, 1974). Comparable surface structures for water penetration have been described for elephants (*Loxodonta africana*, *Elephas maximus*); collecting and spreading of water takes place in numerous small grooves of the granular skin (Lillywhite and Stein, 1987). In the flat bug species *D. lunatus* and *D. magnus*, pillar-like surface structures support the hydrophilic wetting properties and spreading of water (Fig. 4A). Spreading on the surface is slower than within intersegmental channels, but energetically favourable (Fig. 1B). Hence, a passive spreading of water over the body surface is enabled (Hischen et al., 2017).

The penetration of liquids into surface microstructures [also known as hemiwicking (Bico et al., 2002; Quéré, 2008)] has been described as an interplay between pinning and capillary action (Blow et al., 2009). Microstructures within capillary channels can increase capillarity by hemiwicking (Fig. 4B) (Bico et al., 2002). This has been found, for example, as protrusions in skin channels of Australian thorny devils (*Moloch horridus*) (Comanns et al., 2017). In cases in which such microstructures are asymmetric, for example triangular pillars, they can achieve directional penetration of a liquid (Fig. 4C) (Blow et al., 2009). The dynamics of hemiwicking have been described using different approaches, and all approaches contribute to the geometric dimensions of the surface structures one way or another (Bico et al., 2002; Quéré, 2008; Chandra and Yang, 2011).

Capillary transport of water

The spreading of collected water can be interpreted as a straightforward way to distribute water away from a collection

site. However, passive transportation over greater distances requires capillary action. Capillary liquid transport can take place in small cavities, such as tubes, ridges or channels, where the capillary forces dominate other major contributing forces such as viscosity, friction or gravitational force (Berthier and Silberzan, 2010). Corresponding surface structures can be found in the granular skin of some toads and elephants (Lillywhite and Licht, 1974; Lillywhite and Stein, 1987), surface channels of moisture-harvesting lizards (Gans et al., 1982; Withers, 1993; Veselý and Modrý, 2002; Sherbrooke et al., 2007; Comanns et al., 2015), flat bugs (Hischen et al., 2017) and wharf roaches (Hoese, 1981; Horiguchi et al., 2007; Ishii et al., 2013), and cavities between feather structures of sandgrouse (Rijke, 1972; Joubert and MacLean, 1973; Rijke and Jesser, 2011). In the case of moisture-harvesting lizards, transportation in channels avoids wetting much of the body surface and hence losing volume by evaporation from a larger area (Comanns et al., 2011; Yenmiş et al., 2015).

Moisture-harvesting lizards possess a skin channel network between the scales that extends over the entire body surface (Fig. 1C,D). It allows collection and transport of collected water by capillarity. The channels have a width of 100–300 μm in the basal part (i.e. scale hinges), and narrower openings towards the surface, typically <50 μm (Fig. 5A,B) (Withers, 1993; Sherbrooke et al., 2007). In vertical orientation, these dimensions reflect the measured transport distance of 9.9 cm where capillary forces become equal to gravity in capillaries of about 220 μm in width (Withers, 1993).

Theoretically, the channels must be filled for drinking to occur. However, two structural modifications have been found that most likely enable the lizards to drink even smaller amounts of water than are sufficient for complete filling of the channels (Comanns et al., 2015). First, in the pronounced hierarchical channel structure that has been described particularly for the Australian thorny devil, large cavities can quickly absorb water, whereas sub-capillary structures yield an extension of the transport distance by about 39% (Fig. 5C) (Comanns et al., 2017). Water transportation in these skin channels has been modelled using an adapted dynamics function that closely reflects the channel morphology, hence the combination of water penetration and capillary transport (Chandra and Yang, 2011; Comanns et al., 2017). Second, a directional water transport towards the mouth has been found in two desert lizard species, *Phrynosoma cornutum* (Comanns et al., 2015) and *Phrynocephalus horvathi* (Yenmiş et al., 2015), and results from a combination of asymmetric channel geometry and specific network structure: a narrowing of single channels between two neighbored scales yields a local directional water flow,

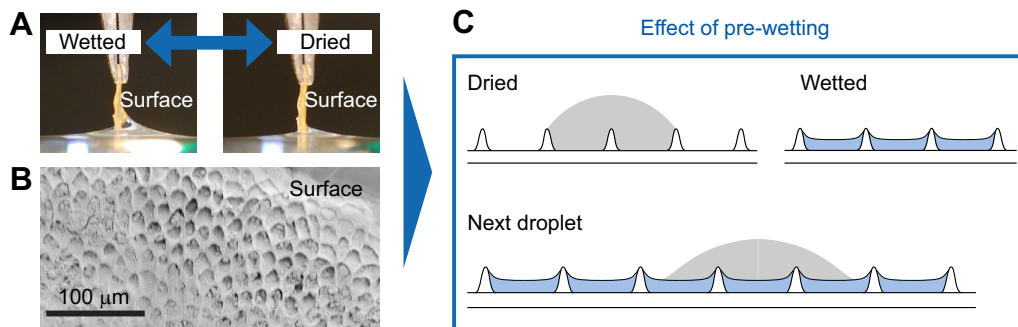


Fig. 3. Pre-wetting to enhance water collection efficiency of moisture-harvesting lizards. (A) A scale of a preserved Texas horned lizard (*Phrynosoma cornutum*) in contact with water in a wetted condition and after drying on silica gel. The effect can be repeated by immersing the scale in water or drying on silica gel, respectively. (B) Scanning electron microscope (SEM) image of a scale surface from the same sample as in A. (C) Model of pre-wetting the hexagonal microstructures on the skin surface. (Images adapted from Comanns et al., 2014, courtesy of WIT Press from Int. J. Des. Nat. Ecodyn. 9, 2014, 206–215.)

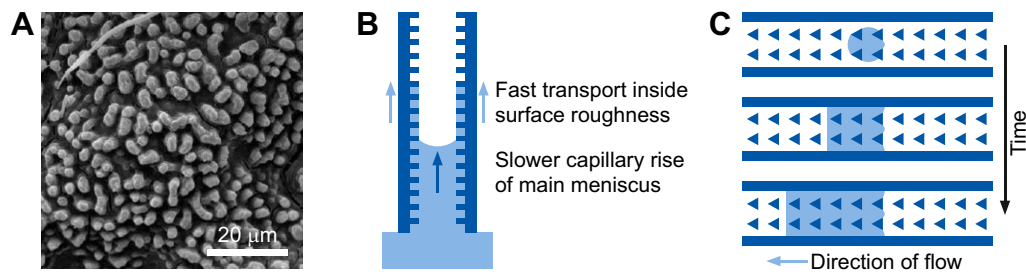


Fig. 4. Structures for water penetration. (A) Pillar-like surface structures of the flat bug *Dysodius magnus* (adapted from Hischen et al., 2017, with permission from Biology Open 2017). (B) Different capillary rises in a capillary tube (after Bicó et al., 2002). (C) Asymmetric pillar structure for directional penetration of liquid and schematic flow of an applied droplet (after Blow et al., 2009).

whereas specific interconnections preclude the inhibition of water transport towards the mouth, but not in the rearward direction (Fig. 5D) (Comanns et al., 2015).

A number of crustacean wharf roaches, such as *Ligia exotica* and *Ligia oceanica*, passively collect water from wet surfaces of their coastal habitat (Hoese, 1981; Horiguchi et al., 2007). Water is then transported in open structures of the cuticle of the legs, which act as capillaries. Further examination has revealed more detail: hair- and paddle-like microstructures on two neighbored legs (i.e. pereopods VI and VII) collect and transport the adhered water; the water is then transported further along the swimming limbs (pleopods) and to the hindgut, near the anus, for uptake by absorption (Horiguchi et al., 2007; Ishii et al., 2013). Collected water also establishes a water film on the integument and evaporation is regularly used for thermoregulation (Hoese, 1981).

Accumulation and storage of water

Various kinds of surface structures can form cavities, in which collected water can accumulate. Such accumulation can be as simple as entrapping rain between the body coils of some snakes from the genera *Crotalus*, *Bothrops* and *Bitis* (Louw, 1972; Robinson and Hughes, 1978; Andrade and Abe, 2000; Cardwell, 2006; Repp and Schuett, 2008; Glaudas, 2009) (Table 1). The collected water is then licked off the body surface. Accumulation of water can also take place in cavities of integumental surface structures of other animals, which has been determined as integumental water holding capacity (Table 2). The highest values have been found for the lizard *M. horridus* (9.19 mg cm^{-2}). Interestingly, the water holding capacity of elephants is much lower (*L. africana*: 1.27 mg cm^{-2} ; *E. maximus*: 0.81 mg cm^{-2}), although the granular skin of elephants has a much coarser structure, with depths up to 5 mm (Lillywhite and Stein, 1987) (Table 2). The difference potentially results from

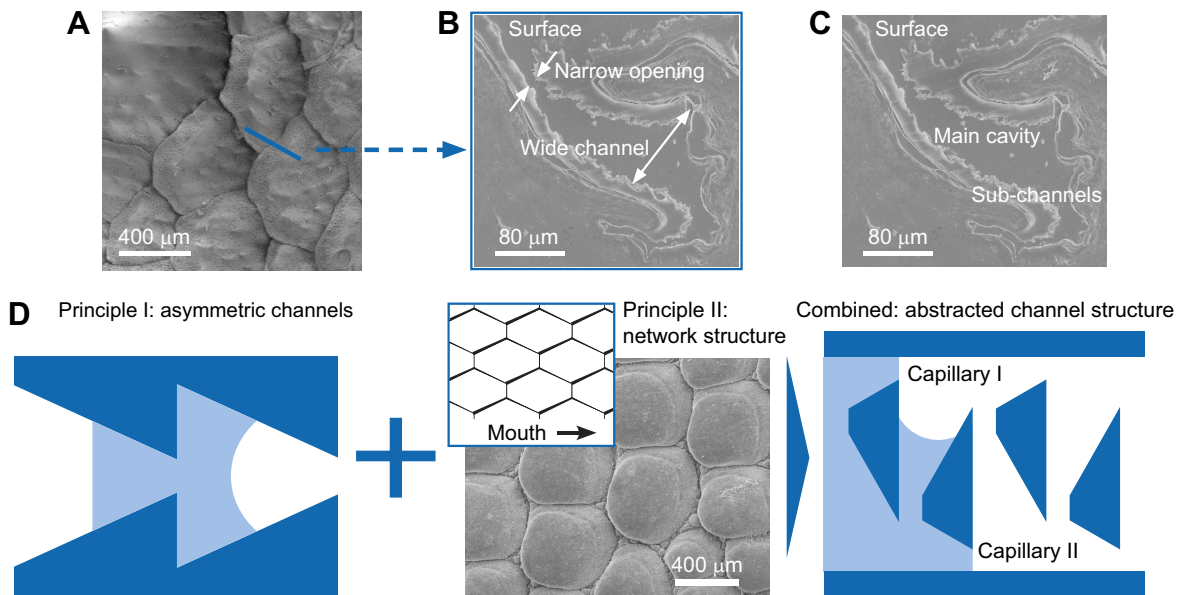


Fig. 5. Channel structures and functionality of water transport on the skin of moisture-harvesting lizards. (A) Overview of the ventral skin of the Australian thorny devil (*M. horridus*). The blue line schematically indicates the position of cutting in B (SEM image from Comanns et al., 2014, courtesy of WIT Press from Int. J. Des. Nat. Ecodyn. 9, 2014, 206–215.). (B) Semi-thin section (0.7 µm) of a skin sample after removal of epon embedding. SEM image is kindly provided by Jenice Linde (RWTH Aachen University). The image reflects the channel dimensions of *M. horridus* in Sherbrooke et al. (2007). (C) A hierarchical channel structure of the main cavity and sub-channels enables a greater transport distance. (D) Functional principles for directional, passive transport of water arising from the skin channel structures of the Texas horned lizard (*P. cornutum*). The narrowing (i.e. asymmetry) in longitudinal direction (principle I) has been abstracted to a saw-tooth-shaped channel. Different curvatures of the liquid–air interfaces yield a local transport directionality. For longer distances than single channels, directionality results from specific interconnections of the channel network structure (principle II), by which an inhibition of water transport is precluded in the forward direction, but not in the rearward direction. A possible combination of both principles is illustrated at the right (combined). [Reproduced from Comanns et al., 2015, licensed under CC-BY 4.0; from Joel et al., 2017, adapted with permission from Springer: Springer Nature, Functional Surfaces in Biology III by S. Gorb and E. Gorb (ed.), ©2017.]

Table 2. Water-holding capacity of the integument surface of some animals

Species	Water-holding capacity (mg cm ⁻²)	References
<i>Moloch horridus</i> (lizard)	9.19	Comanns et al., 2016a
<i>Phrynosoma cornutum</i> (lizard)	5.9	Sherbrooke, 2004; Comanns et al., 2016a
<i>Acrochordus granulatus</i> (snake)*	5.39	Lillywhite and Sanmartino, 1993
<i>Anaxyrus woodhousii</i> (toad)	0.43	Lillywhite and Stein, 1987
<i>Loxodonta africana</i> (elephant)	1.27	Lillywhite and Stein, 1987
<i>Elephas maximus</i> (elephant)	0.81	Lillywhite and Stein, 1987

*Aquatic species.

stronger hierarchical skin structures or a higher density of skin channels in *M. horridus* (Comanns et al., 2017). Furthermore, it is worth noting that the Texas horned lizard *P. cornutum* (5.9 mg cm⁻²) has a similar integumental water holding capacity as the aquatic file snake *Acrochordus granulatus* (5.39 mg cm⁻²; Table 2).

Many sandgrouse species (e.g. *Pterocles alchata*, *Pterocles bicinctus*, *Pterocles namaqua*) have wettable breast feathers to accumulate and store water (Fig. 1E) (Meade-Waldo, 1896; Cade and MacLean, 1967; Joubert and MacLean, 1973). This is in contrast to other birds, where quasi-hierarchical structures of feathers enable water repellence and protection against water penetration (Rijke and Jesser, 2011; Srinivasan et al., 2014). Sandgrouse feed on dry seeds and inhabit mostly arid regions, which demands daily water uptake, hence drinking. Water is carried in the ventral plumage from ponds up to 80 km away in volumes up to 30 ml per flight, i.e. 5–15% body mass, to water the young (Maclean, 1968; de Juana, 1997). In fibrous structures, such as feathers, water is not held by a single (structured)

surface. Future studies may therefore determine the values in relation to the volume of the feathers. The volume of sandgrouse breast feathers is created by a different structure compared with that of other pennaceous feathers (see Glossary): the barbules (radii) are twisted into each other without hooks. In wet conditions, the barbules unfold independently, enclosing the accumulated water volume (Maclean, 1968; Rijke, 1972). Besides suggested reversible physicochemical changes in the feather keratin (Rijke, 1972), the reason for that structural change remains unclear and forms part of current studies (Heiko Schmied, personal communication).

Condensation

Condensation of water vapour into liquid droplets on the animal has been observed for some hylid frogs, such as *L. caerulea* and *P. sauvagii* (Fig. 1F) (Toledo and Jared, 1993; Tracy et al., 2011). The required thermal gradient is achieved by the ectothermic properties and temporal changing of the microhabitat. These frogs

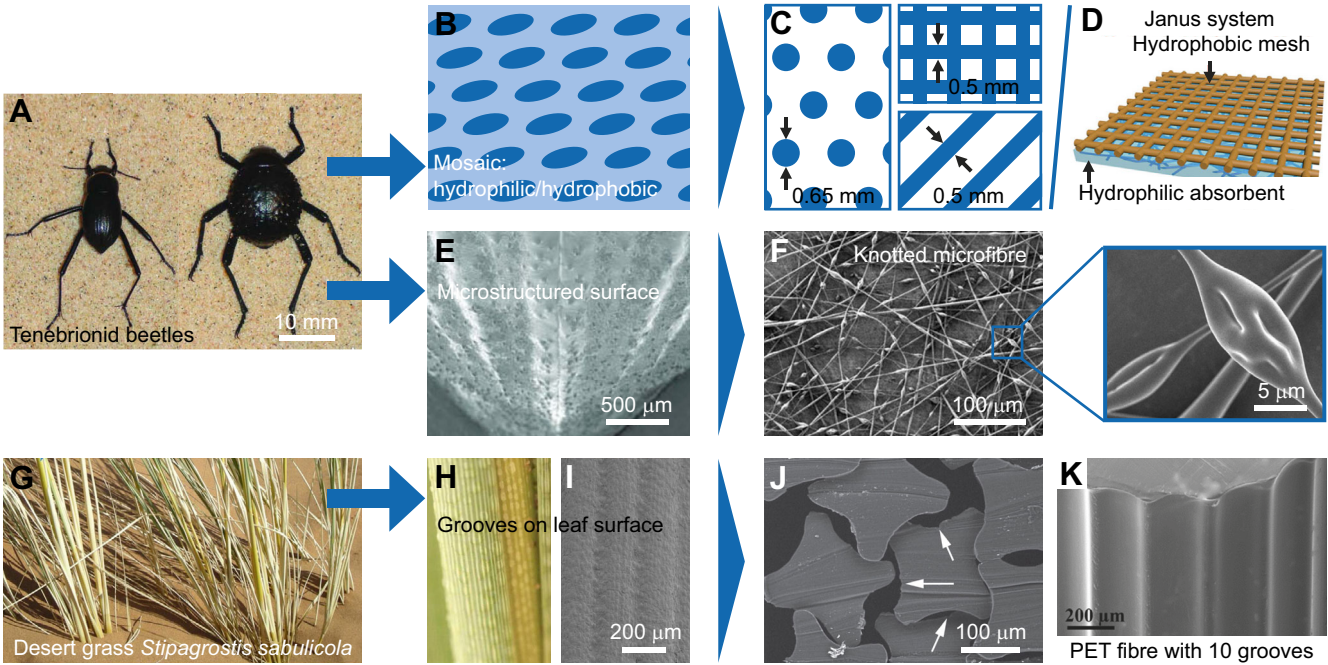


Fig. 6. Examples of fog-collecting surfaces and applications. (A) Tenebrionid beetles from the Namib desert [left: *Onymacris laeviceps*, right: *Physosterna cribripes* (from Nørgaard and Dacke, 2010, ©BioMed Central; reproduced with permission)]. (B) Schematic mosaic of a hydrophobic surface and hydrophilic islands. (C) Mosaic patterns of hydrophobic and hydrophilic areas that have been realized using stainless steel and carbon nanotubes (dimensions reflect estimated values from White et al., 2013). (D) Janus system for fog collection reflects an abstraction of the mosaic surface chemistry of the tenebrionid beetle. Here, fog is collected at the hydrophobic mesh and, after some coalescence, the droplets are absorbed into the hydrophilic material (modified from Cao et al., 2015, ©Wiley-VCH Verlag GmbH & Co. KGaA; reproduced with permission). (E) Microstructured surface of the cover wings (elytra) of *Onymacris laeviceps* (from Nørgaard and Dacke, 2010, ©BioMed Central; reproduced with permission). (F) Microstructured surface of the tenebrionid beetle abstracted to knotted microfibres (from Dong et al., 2012, ©Wiley-VCH Verlag GmbH & Co. KGaA; reproduced with permission). (G) Namib desert grass *Stipagrostis sabulicola* and (H,I) its leaf surface (from Roth-Nebelsick et al., 2012, with permission from the Royal Society). The grooves guide collected fog towards the plant base. (J) Quadrilobal polyamide (PA 6) monofilaments, which reflect the surface grooves abstracted from the leaf surface structure of *S. sabulicola*. Arrows indicate surface irregularities (from Roth-Nebelsick et al., 2012, with permission from the Royal Society). (K) Polyethylene terephthalate (PET) fibre with 10 grooves along the circumference as an example of other fibre cross-sections containing grooves (reprinted with permission from Azad et al., 2017, ©2017 American Chemical Society).

need not only to minimize water loss, but also to take up water. Some species of the above-mentioned genera manage this by passively collecting water present as air humidity (Shoemaker et al., 1972; Toledo and Jared, 1993; Tracy et al., 2011). As ectotherms, the frogs cool down in the open but, when they enter warm and humid tree holes, the temperature difference leads to condensation on the colder body surfaces of the frog. Determined condensation rates have been up to 3 mg cm^{-2} body surface at a temperature differential of 15°C and duration of 20 min; such a rate is higher than water loss by evaporation (Tracy et al., 2011). In combination with the lipid secretions, it is not surprising that speculations have been made regarding the potential role of these secretions for modifying hygroscopic properties and increasing the capability for condensing water (Toledo and Jared, 1993).

Lasiewski and Bartholomew (1969) have surmised that condensation underlies the water ecology of the desert-dwelling spadefoot toads *Scaphiopus hammondi* (synonym: *Spea hammondi*) and *Scaphiopus couchii*. Based on their considerations, it has been speculated that condensation also serves as a potential water source for some moisture-harvesting lizards (Gans et al., 1982; Schwenk and Greene, 1987; Comanns et al., 2011, 2016a). The spikes of the skin, it is thought, act as condensation foci, in particular for dew, which is regularly found in deserts (Gans et al., 1982; Beysens, 1995). Although laboratory conditions facilitate greater condensation than natural habitats, it has been shown that condensation on lizard skin is very unlikely to provide water in sufficient quantities for drinking (Comanns et al., 2011, 2016a). Thorny devils (*M. horridus*) can collect about 0.2% body mass by condensation (Withers, 1993; Comanns et al., 2016a), whereas 0.75% body mass gain by condensation has been reported for the western banded gecko *Coleonyx variegatus* (Lasiewski and Bartholomew, 1969). By comparison, thorny devils have been observed drinking when their skin channels are filled, which relates to a water collection ratio of about 3.2% body mass (Comanns et al., 2016a). However, condensation has been found to be sufficient to pre-wet the skin of the lizards and enable faster collection of water from more-efficient sources (Fig. 3) (Comanns et al., 2016a).

Despite general linguistic usage, fog cannot be ‘condensed’. This is because it comprises numerous fine droplets of already condensed water, light enough to remain suspended in the air (Gultepe et al., 2007). Therefore, fog can be collected without condensation, meaning without a sufficient temperature gradient. Several species of tenebrionid beetles as well as the sand-diving lizard *Aporosaura anchietae* and the viper *Bitis peringueyi* collect fog by exposing their body to fog-transporting wind in the Namib desert (Louw, 1972; Hamilton and Seely, 1976; Parker and Lawrence, 2001; Nørgaard and Dacke, 2010). Tenebrionid beetles of the genera *Stenocara*, *Physosterna* and *Onymacris* exhibit a mosaic of hydrophilic and hydrophobic structures (see Glossary) on the elytra that facilitate the collection of the fine mist from air; the hydrophilic islands act as condensation foci, whereas hydrophobic areas allow accumulated droplets to roll off easily (Hamilton and Seely, 1976; Parker and Lawrence, 2001; Nørgaard and Dacke, 2010). Besides physicochemical properties of the body surface, water collection can be assisted by gravity, i.e. a stereotypic body inclination. However, this behaviour is known only in two species of *Onymacris* (Hamilton et al., 2003).

Utilization of external forces

Some land tortoise species (e.g. *Psammobates tentorius trimeni*, *Kinixys homeana*, *Homopus areolatus*) have been found to benefit from gravity in a quite remarkable way (Table 1). By lifting their

hind limbs, water is channelled between the large ridges on the carapace of the tortoise to the mouth for drinking (Fig. 1G) (Auffenberg, 1963). In effect, the animals expose themselves to an external force, which transports collected water towards the mouth. The stereotypic body posture of most moisture-harvesting lizard species depicted in Table 1 includes similar stretching of the hind limbs and lowering of the head (Schwenk and Greene, 1987; Sherbrooke, 1990; Veselý and Modrý, 2002). Here, gravity appears to be utilized to support the functionality of skin microstructures and channels. Tenebrionid beetles also use their body inclination to let droplets of collected fog roll off their elytra to the mouth for drinking (Hamilton and Seely, 1976; Nørgaard and Dacke, 2010). For *Onymacris unguicularis* the elevation angle has been measured as 23° (Nørgaard and Dacke, 2010).

Biomimetic approaches and fabrication

Passive water collection has inspired a lot of studies, and many of the functional structures that are presented above have been considered for adaptation to technical applications. Particular progress has been made for materials for fog collection, surface structures for directional transport of liquids for various material–liquid combinations, and textiles for separation of oil–water emulsions.

The collection of fog (i.e. condensed water suspended in air) has been considered as a means of water supply in regions satisfying certain criteria. Inspiration for development of ‘fog collectors’ (Shanyengana et al., 2002; Dorrier and Rühe, 2008a; Ahmad et al., 2010) has not only been taken from the mosaic pattern of the cuticle of tenebrionid beetles in the Namib desert, but also several plants (Andrews et al., 2011; Azad et al., 2015a,b). Examples of devices include structured material surfaces (Fig. 6A–D) (Dorrier and Rühe, 2008a; White et al., 2013) or fibres for textile applications (Fig. 6E–K) (Sarsour et al., 2010; Dong et al., 2012; Cao et al., 2015; Azad et al., 2017). Biomimetic approaches are less often found for thermally facilitated condensation. However, higher rates of water condensation have been found for uniformly hydrophilic surfaces (as for tree frogs) than for mosaic patterns of hydrophilic/hydrophobic surfaces (as for tenebrionid beetles) (Lee et al., 2012). The maximum condensation rate of $25 \text{ mg cm}^{-2} \text{ h}^{-1}$ that has been measured for artificial hydrophilic surfaces at a temperature differential of 15°C and 92.5% relative humidity is more than twice the rate that has been found for tree frogs under comparable conditions (Tracy et al., 2011; Lee et al., 2012).

Surface channels can transport water by capillarity. The channels on the legs of wharf roaches have been considered, for example, when designing spacecraft water-management systems (Thomas et al., 2010; Ishii et al., 2013). For two lizard species, water transport in skin channels is directional towards the mouth (Comanns et al., 2015; Yenmiş et al., 2015). In a technical context, directional fluid transport is often referred to as ‘liquid diodes’. Technologies for such microfluidic diodes include movable parts such as flaps (Adams et al., 2005) or cylindrical discs (Sochol et al., 2013). However, inspired by the Texas horned lizard, surface structures have been fabricated for passive, directional transport (Comanns et al., 2015). Channel asymmetry in the longitudinal direction as well as specific interconnections have been abstracted and transferred to materials such as polymethyl methacrylate (PMMA) and steel, maintaining directional transport of water and lubricants, even against gravity for a few centimetres (Comanns et al., 2015, 2016b). Lately, other surface structures for passive, directional fluid transport have been derived from transport of the oily defensive liquid by the flat bug *D. lunatus* (Plamadeala et al., 2017) and from

the morphology of the spermatheca of fleas (Buchberger et al., 2018). All such surface structures for passive, directional liquid transport have been considered to be of particular interest for similar applications, such as in fields of lubrication (Comanns et al., 2016b). Here, the aspect of abrasion plays an important role (Uddin and Liu, 2016). Further considerations have been made regarding heat exchangers, microfluidics, distilleries, e-ink displays and hygiene products (Buchberger et al., 2015; Comanns et al., 2015, 2016b; Buchberger et al., 2018). In general, directional wetting phenomena or transportation have been found to result from directional surface structures or their orientation (Hancock et al., 2012; Xia et al., 2012; Chen et al., 2016).

The utilisation of gravity for water transport can be further abstracted to external forces in general that are within reach and utilizable for fluid transport. For example, the movement of machine components can be used to passively transport lubricants into bearings (Sathyan et al., 2011).

As described above, sandgrouse can store water enclosed within their breast feathers (Rijke, 1972; Joubert and MacLean, 1973; Rijke and Jesser, 2011). Another, rather different, mechanism of liquid storage in fibrous systems has been described for oil bees (Buchmann, 1987; Schäffler and Dötterl, 2011); here, branched, hair-like protrusions of the cuticle with oleophilic (see Glossary) properties collect and store the oil from flowers (Rüttgers et al., 2015). Investigations of this mechanism have led, for example, to the development of textiles for oil collection from sea water (Yao et al., 2011). The separation of emulsions is also possible with coated textiles, such as a Janus membrane and others (Feng et al., 2004; Tian et al., 2014; Brown and Bhushan, 2015).

In general, investigations of biological role models provide knowledge about the specific functionality reflecting adaptations to the conditions of the environment of the animals. Adaptations involve a compromise between parameters of various influences and requirements on the animal body surface. Abstraction and transfer to artificial surface structures reduces such compromises, but limitations occur in the challenge of other restrictions; for example, relating to specific conditions of the technical environment.

Transferring abstracted functional principles of wetting phenomena, water collection or water transport to artificial materials commonly requires fabrication of rather filigree structures in the micrometre range. This is non-trivial, but several technologies have been used to fabricate with sufficient accuracy; for example, direct laser structuring (see Glossary) (Klocke, 2007; Poprawe, 2011; Chen et al., 2013; Comanns et al., 2016b). For somewhat larger structures, micromilling (see Glossary) might be considered (König and Klocke, 2002; Biermann and Krebs, 2011), whereas large areas could require methods such as replication, embossing, injection moulding and additive manufacturing (Abbott and Gaskell, 2007).

Concluding remarks

The ability to collect water using the integument serves as a major adaptation of several animal species to their dry habitat to aid coping with conditions of limited water supply. The complex nature of surface structures itself suggests an important adaptational role of passive water collection performed by the integument. The morphology and function of integumental structures also show some convergence in this regard for the species considered above.

Passive water collection involves hydrophilic surfaces, at least to some extent, and one could even argue that wettable surfaces (contact angles <90 deg) might be required for such ability. Surface structures are similarly involved in water collection, and two conclusions can be made. First, all structures appear to

significantly increase the body surface area responsible for collecting water from the animal's environment. This is less pronounced in the case of fog-basking beetles where surface chemistry plays a more important role. Second, the structures appear to offer specific functionality: different kinds of micropillars or hexagonal micro-ornamentation can alter the wetting properties of the integument in order to subsequently obtain some degree of spreading, grooves or channels can collect and transport water, and hair-like structures are found in the cases of accumulation and storage of water.

Although many species exhibit an accompanying behaviour – that is, active body movements – the actual process of water collection remains passive. The behaviour can instead be regarded as positioning the body surface towards the source from which water is obtained or to assist gravity-mediated water collection.

If we investigate biological role models, we often find specific functionality reflecting adaptations to the conditions of the animal's environment. Such specific functionalities, especially those resulting from surface structures, can be used for biomimetic approaches. Many of the described structures have been considered for technical applications, in particular mosaic patterns to collect fog for water supply, and surface channels to improve lubrication, micro-fluidics or hygiene products.

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Competing interests

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