

## Review



**Cite this article:** Cloete E, Khumalo NP, Ngoepe MN. 2019 The what, why and how of curly hair: a review. *Proc. R. Soc. A* **475**: 20190516.  
<http://dx.doi.org/10.1098/rspa.2019.0516>

Received: 10 August 2019

Accepted: 16 October 2019

**Subject Areas:**

biomechanics, biochemistry, materials science

**Keywords:**

curly fibres, curly hair research, curvature fibre model, hair biology, human scalp hair

**Author for correspondence:**

Malebogo N. Ngoepe

e-mail: [malebogo.ngoepe@uct.ac.za](mailto:malebogo.ngoepe@uct.ac.za)

# The what, why and how of curly hair: a review

Elsabe Cloete<sup>1</sup>, Nonhlanhla P. Khumalo<sup>1</sup> and Malebogo N. Ngoepe<sup>2</sup>

<sup>1</sup>Hair and Skin Research Lab, Division of Dermatology, Department of Medicine, Groote Schuur Hospital and University of Cape Town, Cape Town, South Africa

<sup>2</sup>Department of Mechanical Engineering, University of Cape Town, Cape Town, South Africa

EC, 0000-0003-2125-8564; MNN, 0000-0002-3639-9063

An attempt to understand and explain a peculiarity that was observed for curly fibres during experimentation revealed disparate literature reporting on several key issues. The phenotypical nature of curly fibres is only accurately understood within the larger scope of hair fibres, which are highly complex biological structures. A brief literature search produced thousands of research items. Besides the large amount of information on the topic, there was also great variability in research focus. From our review, it appeared that the complexity of hair biology, combined with the variety of research subtopics, often results in uncertainty when relating different aspects of investigation. During the literature investigation, we systematically categorized elements of curly hair research into three basic topics: essentially asking why fibres curl, what the curly fibre looks like and how the curly fibre behaves. These categories were subsequently formalized into a curvature fibre model that is composed of successive but distinctive tiers comprising the elements in curly hair research. The purpose of this paper is twofold: namely to present (i) a literature review that explores the different aspects of curly human scalp hair and (ii) the curvature fibre model as a systemized approach to investigating curly hair.

## 1. Introduction

A quick review of current and most recurrent topics addressed in hair research includes hair growth, loss, corrective practices/surgery, mechanical, physical and chemical properties, follicle morphology and activities,

genetic controls, forensic investigations and clinical pathology [1–8]. The phenotypical nature of the curly fibre is explored by some, but, compared with the bulk of the investigations, the curly fibre is mostly an addendum in the field of hair research. The work presented in this paper arose from an interesting phenomenon observed during tensile studies of hair fibres of different degrees of curliness, in which curly fibres lost a significant degree of curl during the preparation process. Exploring the observed phenomenon in light of available theories and experimental findings on curly hair, a literature review revealed a diversity of intentions and investigation perspectives when studying hair in general (all scalp hair forms). It also became evident that, in many of the reports, there was a gap in the comprehensive understanding of how certain aspects under investigation relate to one another or to other important aspects relating to the hair fibre. This lack of interconnectedness is not unusual for an interdisciplinary field, but nonetheless produces inappropriate associations or combinations of non-parallel concepts. This is especially true for curly hair fibres, where phenotype is usually described in race-dependent hair subjective terms.

The main purpose of this paper is to present a literature review that explores the different aspects of curly human scalp hair. This review aims to address three main questions which have shaped the field: what does curly hair look like (structurally), why does some hair curl and how does curly hair behave? To answer any of these questions, it is necessary to distinguish between the different macroscopic parts of a fibre, irrespective of its shape. Each hair fibre comprises two distinct portions: namely, the growing and the keratinized portions. Below the scalp, the growing portion is generated in the follicle; above the scalp, the keratinized portion exists as a dead biological structure. The terms more commonly used for the keratinized part are ‘hair shaft’, ‘hair fibre’ or simply ‘fibre’. Since hair curliness is generated in the growing portion, the ‘why’ question of the literature review is addressed at the follicular level. Curly fibre behaviour (the ‘how’ question) pertains mostly to the keratinized portion. The ‘what’ question requires an answer for both growing and keratinized portions.

Answering these questions through the literature review has led to the development of a curvature fibre model that formalizes successive but distinctive tiers of elements in curly hair research. This model is presented in the final part of this paper. The model offers researchers a tool to obtain an overview of the available relevant research focus areas; it also assists with comparative studies on curly hair and highlights areas in which more research is required. It helped us to identify where a theory about the observed phenomenon would belong within the myriad of curvature aspects, and, from that point, enabled the development of new theoretical constructs to explain the observed phenomenon. While the explanation for the observed phenomenon is important, it is not the focus of this paper, but is described elsewhere as part of a larger research project described in [9].

## 2. Review of curly hair research

Before presenting the literature review, the currently used race-based taxonomy is briefly visited to shed light on the interpretation of results from various studies. Other taxonomies are presented in the main review of the ‘what’ question.

Current broad references that are used in hair research are African, Asian or European hair. Broadly speaking, ‘African hair’ refers to hair of individuals with ancestry from Africa; ‘European hair’ refers to hair of individuals with ancestry from Europe; and ‘Asian hair’ refers to hair of individuals with Asian ancestry. Since the above classification excludes many unique hair type groups, other classifications have appeared in recent years, such as distinction between East and West Asian hair, in which ‘East Asian hair’ tends to refer to hair obtained from individuals from China and eastwards, whereas ‘West Asian’ refers to individuals predominantly from Middle Eastern countries. Hair from populations not fitting the above classification descriptors is usually designated by their country of origin, e.g. ‘Mexican hair’ or ‘Tunisian hair’ or ‘Australian hair’, but publications on these populations are relatively infrequent.

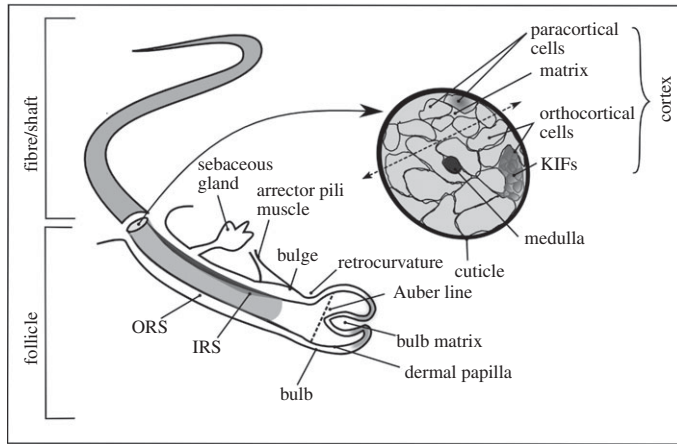
The terms 'European hair' and 'Caucasian hair' are often used interchangeably and are taken to denote 'wavy' to 'straight' hair; 'East Asian' hair is taken to mean 'pin-straight' hair; and 'African' or 'ethnic' hair is taken to signify 'curly' or 'very curly' hair. A variation of 'African hair' is 'Afro hair' and afro-textured hair, to signify 'very curly' hair. These assumptions are essentially flawed since many individuals from both of the first two groups have curly hair. While the degree of curliness among Europeans and Asians is generally lower than that in Africans, some Europeans and Asians have kinky or very curly hair. From genotyping results, European hair shape varies mostly between wavy (46.6%) and straight (40.7%), with some curly hair (12.7%) ( $n = 2138$ ) [10]. The same study showed that Asian (East and West) hair shape is also mostly straight (46.7%) or wavy (41.3%), with some curly hair (12%) ( $n = 92$ ). However, African hair shape is mostly curly (94.9%), with some wavy hair (5.1%) ( $n = 39$ ). No distinction was made between degrees of curliness or waviness, or whether 'stick straight' and 'near straight' were regarded as similar. An important fact indicated by the study is the high incidence (greater than 50%) of non-straight fibres in individuals of European and Asian ancestry. Another important fact about curly hair was the large variability in the degree of curl among individuals of African ancestry [11,12]. From these studies, it became clear that a single curl cluster for 'curly hair' is specious. Hair-specific taxonomies are described later in this paper. Of relevance to the immediate discussion is an awareness of terminology that is used in curly hair research.

As demonstrated in the review presented below, the majority of published studies used fibres from African ancestry as a prototype of curly hair. Some studies (described later) considered fibre curliness as a race-independent descriptor, but these were minimal. Research results for 'curly fibres', based only on samples of African ancestry, present genotypic fibre features as though they are phenotypic, being representative of all curly fibre features. The reverse of this statement is also true, where attributes that are true for the phenotype are credited to the genotype. For example, African hair fibres are popularly thought to have lower fibre strength and stress break loads [13–15], lower lustre [13], a higher friction coefficient [16] and higher lipid content [17,18] than European or Asian hair. There is a possibility that these attributes may be true for all fibres that deviate distinctively from a straight line, irrespective of ancestry. A few (interracial) studies on curly fibres have indeed found that some characteristics previously attributed to race are independent of ancestry [19–22]. Preliminary work from our own studies and experience also concurs with findings that suggest that the intrinsic 'curved' hair is a separate phenotype that has distinct physical, biological, mechanical and chemical features. From our review, there is little research data available on curly fibres from individuals of different ancestries. Furthermore, the available studies that used curly hair from one or two individuals of non-African ancestry are too limited in scope to generalize the results. While some of these small sample studies are proof-of-concept investigations, the scientific reliability of data based on such small sample pools needs to be confirmed to account for variabilities.

For the purposes of this paper, we accepted the deficiencies described above as a given limitation. In seeking to answer the three questions through the literature review (i.e. 'what' does curly hair look like (structurally), 'why' does some hair curl and 'how' does curly hair behave), it was necessary to separate the various research activities on curly hair into sensible categories. While many of the elements in a single category or even across two categories may interweave, a pattern presents itself nonetheless. Since a description of the hair is required to explain the structural and biochemical environments wherein the 'why' and 'how' questions are answerable, curly fibre characterization ('what') is presented first.

### (a) What is the structure of a curly fibre?

Below the scalp, the structure of the follicle and growing fibre is inextricably linked to follicular activities. Above the scalp, the visible fibre has physical (macroscopic) properties that are supported by underlying mechanical characteristics: physical (micro- and nano-) structures assuming distinct geometries and biochemical composition. Figure 1 shows the anatomy of the curly hair, with attention to the follicle, from which a curved fibre grows, as well as a cross-section



**Figure 1.** Structure of a curly hair fibre, showing detail of the growing and keratinized parts. KIF, keratin intermediate filament.

of the fibre (left) that protrudes through the scalp. These portions are described in greater detail in the paragraphs that follow.

### (i) Follicle characterization

While the activities and fundamental roles of the different follicular components are not yet fully understood [23], the follicle morphology is reasonably well described. This synoptic overview (summarized from comprehensive descriptions in [24–28]) presents a basis for elucidations pertaining specifically to curly fibres. Histologically, the follicle is a composite structure, comprising two main compartments, with the connective tissue sheath (CTS) of the outer mesenchymal compartment encasing the inner epithelial compartment. The CTS generates and maintains the other component of the mesenchymal compartment, namely the dermal papilla (DP). Sitting embraced by the bulb matrix at the follicle base (figure 1), the DP is key in fibre production. The epithelial compartment is composed of the bulb matrix, inner root sheath (IRS), outer root sheath (ORS) and the growing fibre. At the widest part of the DP, the Auber line distinguishes between proliferation activities in the lower bulb and differentiation activities in the upper bulb. Differentiation produces the IRS, ORS and the fibre. The IRS and ORS are rigid, multi-layered structures that appear to have a topographically guiding role for the growing fibre. Forming the outer epithelial envelope at the junction with the CTS, the ORS extends up to the follicle orifice. The IRS, on the other hand, forms an interlinked anchoring base with the growing fibre and extends to the bulge area. Beyond this point, the IRS is shed to separate the fibre from the follicular wall. The bulge, being one of the stem cell reservoirs that sustain lower follicle growth, sits at the isthmus of the follicle. The bulge area is also the attachment site of the erector pili muscle.

Early studies (dating back to 1873) on follicle morphology described a direct correlation between follicle shape and race, with distinct curvature (versus collinearity) observed in follicles from African versus European ancestries [29]. Modern studies have shown that the basis of this relationship is phenotypical and not racial [21]. It has also been demonstrated (*in vitro* and *in vivo*) that curly fibres, emerging angularly from the scalp, are generated by curved follicles (that have a retrocurvature at the bulb). Non-curly hair, on the other hand, emerges from collinear follicles that are embedded at approximately right angles with the scalp [21,30,31]. Besides having a curved follicle contour, the bulb, IRS, ORS and CTS of curly fibres also exhibit an asymmetry in shape or cellular distribution, as opposed to symmetry and homogeneous cellular dispersal in non-curly fibres [21,31,32]. In the curly fibre bulb, Ki-67-positive matrix cells are visible above the Auber line on the convex side of the matrix. These cells have a homogeneous spread below the Auber line for

straight hair. More pronounced cellular expressions can also be seen in the CTS, IRS and ORS on the follicle concave side of the curly hair. In straight hair, the CTS, IRS and ORS structures have a symmetrical lengthwise appearance. Evidence of asymmetrical expression of certain keratins and enzymes is also seen in curly fibres, whereas expression in straight fibres appears to be symmetrical. For example, there is evidence of more pronounced concave side expression of K14 and transglutaminase-1 in the ORS and IRS, respectively [31]. Similar dissymmetry of fibronectin glycoprotein has been shown in the CTS [21]; K82 (hHb2 keratin) in the early forming cuticle [31]; and K38 (hHa8 keratin) in the follicle bulb [21]. K38 is also more pronounced in the curly fibre follicle, against the sparse, homogeneous distribution of K38 in the straight fibre follicle [21]. Expression of growth factor insulin-like growth factor-binding protein 5 (IGFBP-5) has also been seen to be significantly higher in curly than in straight fibres [32].

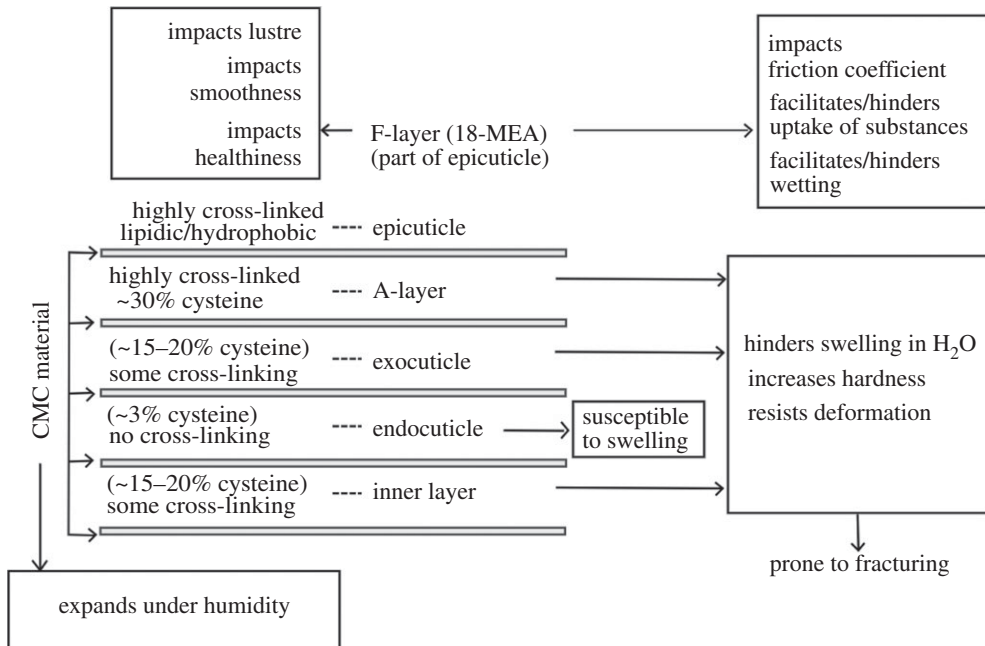
## (ii) Microscopic fibre characterization

As with the follicle, a broad synopsis (summarized from [33–35]) of the fibre is necessary to provide context for discussion. Forming in the follicle, the keratinized fibre protrudes above the scalp. Biochemically, the fibre is characterized by its proteins, lipids and cellular environment. Proteins form the major biochemical component, with the polypeptide backbone (comprising planar amino acid residues) being the basic structural unit of all fibre proteins. The protein backbone may be folded into an  $\alpha$ -helix or various  $\beta$ -strand secondary configurations. Keratin proteins (KPs) comprise various  $\alpha$ -helical-folded backbones that are iteratively aggregated lengthwise (driven by hydrogen and disulfide bonding) to form fibrous structural units. Keratin-associated proteins (KAPs) mostly assume a combination of secondary configurations, including  $\alpha$ -helix strands,  $\beta$ -strands,  $\beta$ -sheets and  $\beta$ -turns [36,37]. The main components of the fibre are composed of KPs and/or KAPs, forming the cuticle, cortex and the medulla. A detailed description of each of these components, as pertains to curvature, is presented below.

*Medulla.* Not found in all hair fibres, the medulla (in the fibre centre) is predominantly present in coarser hair fibres. In an old study on various ethnic groups in India, with hair varying from straight to frizzly, discontinuous medullary cells were found in all hair types, a continuous medulla was found in straight and medium curly (narrow wavy) hair, but absent in frizzly hair (among the test group), and the absence of a medulla was also reported in all hair types [38]. No newer studies that relate fibre curliness to the medulla appear to be available. Further discussion of the medulla is therefore excluded from this review.

*Cuticle and lipids.* The cuticle is mainly composed of KAPs and lipids. The cuticle acts as a protective fibre envelope and comprises several cellular layers that are meshed in cell membrane complex (CMC) material. Cuticle layers may be broadly divided according to main functionality (figure 2). The outer layers (A-layer, exocuticle, endocuticle) fortify the fibre against mechanical and chemical stresses; the lower layers (lower  $\beta$ -layer,  $\delta$ -layer and upper  $\beta$ -layer) form cuticular CMC material. CMC material, although different in chemical composition, is also found at the cuticle–cortex junction and in the cortex itself. CMC material is composed of cell membrane proteins, sandwiched in endogenous lipid layers. These are different from surface lipids exuded from the sebaceous gland in the follicle sac. Lipids are present in both the cuticle and the cortex. Primary endogenous lipids include fatty acids, cholesterol, ceramides and 18-methyl eicosanoic acid (18-MEA) [39,40]. The most well-known hair lipid is 18-MEA (in the cuticle), which forms a covalently bonded monolayer between the membrane protein on the one side and an electrostatic association with fatty acids on the other side to construct cuticle CMC [41]. Cuticle–cortex CMC material has a covalent thioester, polar and salt linkage hybrid character.

Lipids contribute strongly to the fibre's resilience against certain extrinsic stresses, and they also facilitate or hinder substance uptake (both internally and environmentally). Lipids are (to a lesser extent) also associated with fibre stiffness and tensile strength [42], but generally not with fibre curvature. Some studies have suggested that lipids may play a structural role in fibre shape [17,18,40], but no definite expositions have been offered. In lipid characterization studies, two publications reported that African hair contains more internal lipids than European or Asian



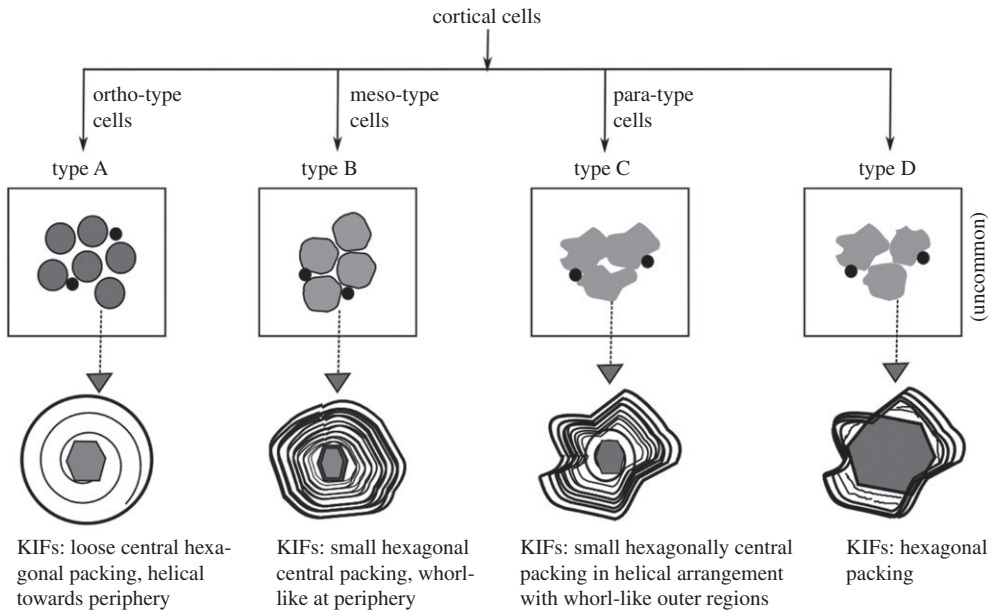
**Figure 2.** Composition of the hair cuticle. Each constituent layer makes a contribution to the physical behaviour of the fibre.

hair [17,18]. In another publication, Asian hair was indicated to have the highest internal lipid concentration when compared with European and African hair [43]. The conflicting statements may be explained by considering the challenges when investigating fibre lipids. Comparative studies on hair lipids are challenged by disproportionate requirements to extract free lipids (easy) and covalently bound lipids (complex), as well as the impact on fibre properties of a delipidized fibre [44]. As a result, ignorance of these challenges during experimentation, or comparing population data with results from other publications that used different extraction methods, may lead to biased characterization and inferences about fibre behaviour.

*Cortex.* The cortex is generally associated with fibre curliness. A detailed review of the hair cortex is presented in [13]. Accordingly, the cortex forms the greater part of the fibre and comprises KPs that are embedded in an amorphous space, called the matrix. The matrix is composed of KAPs and other structures not relevant here. KPs are rigid, fibrous, hydrophobic structures, whereas KAPs are globular, water-soluble proteins, with a hydrophobic interior and hydrophilic surface. While the matrix has an amorphous form, it establishes a coherent nano-structural base for the KPs [45–47], which direct cellular organization during fibre formation.

*Keratin proteins in the cortex.* Dominating keratin intermediate structures that are of interest to this work include the intermediate filament (IF), microfibril (MF) and cortical cell. Summarized from [13,14,48,49], each of these structures is chemically cross-linked with one another and with KAPs of the surrounding matrix. Cortical cells comprise aggregated MFs, which in turn comprise aggregated IFs. Borrowed from wool fibres, morphological distinction is made between three types of cortical cells, namely orthocortical (OC), mesocortical (MC) and paracortical (PC) cells.

Cortical cells have elongated longitudinal (rod-like) shapes and round-to-amorphous transverse shapes. OCs are larger than PCs. The ultrastructural arrangements inside mature cortical cells vary widely. OCs are composed of many small, well-defined MFs, comprising IFs that are tightly packed in annular shape from the cell centre outwards. PCs contain fewer but larger MFs with poorly defined edges. These are arranged around the periphery of the PC, with cytoplasmic remnants located towards the cell centres. In PCs, structures are loosely packed amidst a large amount of matrix material, and IFs assume hexagonal packing. Packing density

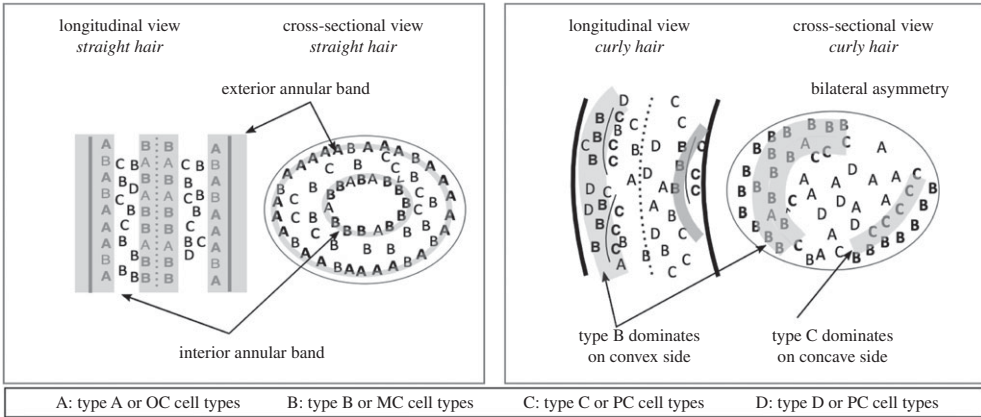


**Figure 3.** Illustration of the different cortical cell types. The packing of the IFs inside the cell contributes to the shape of the cortical cell (adapted from [52,53]).

is higher in OCs than in PCs. MCs appear to be intermediates between OCs and PCs. MCs are not always regarded as a distinct cell type [50,51]. Some studies consider MCs as part of the PC group while others propose two types of OCs, where the description of less-dominating OCs subscribes (to some extent) to that of MCs. The ultrastructure of MCs appears to be a migration from OCs to PCs, with larger size (circular to amorphous) MFs around the cell periphery. In MCs, IF packing is more similar to packing in PC macrofibrils, i.e. near hexagonal, but the small amount of matrix material corresponds more closely to that of OCs.

Some researchers have moved away from the OC/MC/PC designations that originate from wool research. For example, studying naturally straight and curly fibres from Japanese females [52,53], types A–D were designated to cortical cell types. Types A and B resemble OC-like cells, with type B tending towards the description of MCs. Types C and D resemble PC-like cells, with type D an infrequently occurring cell type that is distinct from, yet most like, PCs. Figure 3 illustrates the different cell types and how the keratin intermediate filament (KIF) packing inside each cell impacts both the cell shape and degree of freedom when packed inside the cortex. A surprising element of this study was that, against the accepted premise that East Asian (in this case Japanese) hair is ‘straight’, the study reported that 47% of the sample pool ( $n = 230$ ) had curly hair, varying in curl radius from 0.6 to 16 cm. Studying the ultrastructural arrangement of fibres, the authors observed the presence of four cell types (A–D) in fibres from all hair types. Furthermore, cortical cell types B and C (MC-like and PC-like cells) were found to be the dominating components in all hair. In curly hair, geometric arrangement was distinctly bilateral, with more type C cells on the concave side and more of types A and B on the convex side. The study confirmed the correlation between curvature and bilaterality, and also highlighted the variability and complexity of cortical cell arrangements.

OCs are often described as the dominant cell type in the OC:PC ratio, but significant ratio variability has been reported [54]. More recently, the differences in OC:PC ratio between African, European and Asian hair fibres were demonstrated to be small [51], suggesting weak correlation with both ancestry and curliness. The notion also concurs with the view described in [55]. Even though there is considerable intra- and inter-variability [56], a common ultrastructural feature of very curly fibres is the bilateral symmetry of OCs and PCs. However, a clear increasing



**Figure 4.** Cross-sectional and longitudinal cortical cell distribution in straight and curly hair fibres (adapted from [52,53]).

relationship has been shown for the proportion of OC cells versus fibre diameter in wool [56]. The mathematical relationship was shown to be either linear or log-linear, i.e.  $A = \beta_0 + \beta_1 d$  and  $A = \beta'_0 + \beta'_1 \ln d$ , where  $A$  is the percentage cross-sectional area of OC cells and  $d$  is the cortex diameter. This relationship was found to hold generally true across breed and despite physiological influences such as nutritional stress. Other structural geometries in less curled fibres are uni- or bilobate (dominating OC cortex infiltrated with longitudinal lobe of PCs or MCs) or unicellular [56]. In the bilateral symmetry, OCs and PCs assume convex and concave sides of the curl, respectively (figure 4). MCs appear to be important in intermediate and lower curled fibres [57]. While the OC content shows small variations, there appears to be a significant lean towards an MC/PC combination instead of only PCs [21,56]. The reported concentration of MCs was shown to correlate inversely with curvature, with a complete lack of MCs in very curly fibres [21].

The bilateral arrangement of OCs and PCs is sometimes described as a mechanism, or as a cause of fibre curvature [52,55]. Recent work has indicated that cortical cell lengths are longer on the convex than on the concave sides of the fibre curl [55]. As such, the authors contested the notion that bilaterality causes curvature, but rather argue that cortical cell length is more likely to have a causal relationship with curvature than cell type or ratio. This premise is more accommodating of observed variations in geometric arrangements than the first. However, both dimensional and pattern data describe 'appearance'. There is a need to distinguish between causation and appearance. 'Causation' answers the 'why' question, whereas 'appearance' describes observed structures and patterns, i.e. the 'what' question. The 'bilateral pattern' is a description of the physical appearance of the cortex as viewed microscopically. Observations of bilaterality do suggest certain underlying machinery (apparatus) and processes (mechanisms) that produce cortical cells, which are arranged in a particular cortical cell pattern and which have a particular ultrastructural display. The underlying machinery and processes are the causative factors and not the observed patterns (appearances) that result from the underlying production line, i.e. the ultrastructural arrangement, bilateral pattern and cortical cell lengths are the result of the molecular assembly processes of IFs, MFs and cortical cells [58,59]. It is also necessary to take into account that, besides huge variability of cortical cell patterns (as observed in different sheep breeds), bilateral arrangements have also been observed in the cortices of linear (straight) wool samples. Furthermore, research has demonstrated an inverse correlation between average fibre diameter and propensity to a bilateral pattern [56]. This implies that the relationship between bilaterality and fibre curliness cannot be taken as injective or as causation of curvature. In a certain sense, the observed structures, patterns, cell lengths and ratios lie at the junction of the 'why' and 'what' questions. Yet, the purpose of this work is to present a platform from where equivalent theories can be understood and compared in order to highlight knowledge gaps and focus investigations. Therefore, from a multi-disciplinary viewpoint, engineering and manufacturing



principles would suggest that ultrastructural dimensions and arrangements belong to the ‘what’ question asked about curly hair.

*Keratin-assisting/associating structures in the cortex.* Similar to cortical cell KPs, distinction (motifs and sequence homology) is also made between different KAPs [60], which are, therefore, described in terms of their function and biochemical character. KAP types and quantities vary significantly in different fibre structures, be it cuticle layers or cortical cell types [33,34,58]. KAPs are broadly classified as high sulfur (HS), ultra-high sulfur (UHS) or high glycine–tyrosine (HGT) proteins. The amount of cysteine (more or less than 30 mol.%) dictates the difference between HS and UHS KAPs, whereas HGT proteins have a glycine or tyrosine content of approximately 35–60 mol.% [59]. HS KAPs dominate in the matrix. Cuticles are cysteine and glycine rich [61], with the outer layers comprising highly cross-linked UHS-type proteins and the endocuticle mostly composed of low-sulfur residues and acidic and basic proteins. Cuticular KAPs are high in cysteine, serine, glycine and proline content [13,33–35]. Biochemically, cortex KPs are low-sulfur structures, with a high concentration of basic and acidic residues when compared with cuticular proteins [62]. KPs are also low in proline [63], which is detrimental to the  $\alpha$ -helix structure. In wool fibres, concentrations of cysteine, cysteic acid, threonine and proline were shown to be higher in PCs than in OCs, whereas tyrosine, glycine, phenylalanine and leucine were dominating in OCs [64,65]. In certain but not all studies [65], aspartic acid concentrations have also been found to be dominant in OCs.

### (iii) Macroscopic characterization of the fibre

On a macrolevel, hair curl taxonomies provide a meaningful tool for making scientific sense of, and deriving objective inferences from, hair study results. A classic taxonomy paper, proposed to move away from race-based fibre classification, is the segmentation tree analysis method (STAM) [20]. Based on curvature phenotyping, STAM classifies hair into eight curl-type groups (I—straight to VIII—tightly curly). STAM introduced a significant shift by considering hair fibres phenotypically, rather than racially. However, it poses complexity and repeatability challenges. When working with large sample pools (e.g. 6000 in [66], 26 964 in [67] and 9674 in [10]), STAM is tedious and complex when phenotyping medium to very curly fibres. Using STAM, a high inter-rater variability has also been demonstrated for very curly hair [68]. Accordingly, a modification has been suggested to STAM, whereby classes V and VI as well as VII and VIII are collapsed into single groups each. The modified-STAM taxonomy demonstrated significantly reduced rater variability when compared with the advantages of having more curl classes, at least when considering the current knowledge on how fibre features correlate with different degrees of curvature. The literature review showed that the uptake of STAM/modified-STAM (mostly in material, mechanical, structural and cosmetic sciences) as a methodology is relatively low and that most publications still use race/population as the phenotypical fibre discriminant. A similar taxonomy to the modified-STAM has been observed in genetic and forensic sciences, using a six-point scale system to differentiate between ‘stick straight’, ‘straight’, ‘wavy’, ‘big curls’ and ‘small curls’ [10,69]. An even more simplistic model uses a three- or four-point scale system, in which case differentiation includes ‘straight’, ‘wavy’, ‘curly’ and/or ‘frizzy’ hair [10,66].

Demonstrated in [11,12], curly fibres (of African descent) vary widely in degree of curliness. Furthermore, distinct correlation has been demonstrated between fibre curliness and certain features (e.g. curliness and diameter, curliness and elastic limit) [11,52,53]. This indicates the necessity to differentiate between degrees of fibre curliness in order to gain a more accurate understanding of hair fibres. In our opinion, a practical taxonomy needs to be uncomplicated to facilitate easy, yet accurate, use. The above-mentioned six-point scale [69] and modified-STAM [68] appear to support these requirements. More appropriate descriptions, for straightforward classification of large datasets, could be ‘stick straight’, ‘near straight’, ‘wavy’, ‘wavy, big curls’, ‘small curls, frizzy, kinky, afro’, ‘tight, interwoven small curls’.

While it may be tempting to group ‘straight’ and ‘near-straight’ fibres into one group, there seem to be differences between ‘stick straight’ and ‘near-straight’ fibres. A study that points out

the importance of differentiation is described in [70]. Volunteers were 151 individuals of European ancestry who donated 20+ hair fibres each; these were then classified as types I–IV according to STAM. The aim of the study was to evaluate factors (instrumentally and via survey) that contribute to the perception of ‘fine hair’. Accordingly, there was a strong correlation between self-perception of ‘fine hair’ and low average fibre diameter, hair density, stiffness and break force load. Statistical analysis showed that hair at a STAM class threshold of 2.5 (below III, but above II) fell in the category of ‘fine hair’, whereas hair above this threshold was categorized as ‘not fine’. Fibres in the latter group were thicker, stronger and stiffer, with a greater scalp density. This means that curlier hair was found to be thicker, stronger and more resilient under mechanical forces than the near-straight hair. How features of the hair at the top of the spectrum (classes III and VI) of the tested group would compare with features at the low end of the spectrum for curly African fibres (class IV) is unknown. However, what is interesting from this study is the seeming decrease in quantitative results from class I (stick straight) to class II (straight), followed by an increase in class III (wavy). Based on the mechanical trends observed for various fibre properties (average diameter, ellipticity and straightness), high torsional rigidity and strength are anticipated for mechanical structures (fibres) that are similar to cylindrical beams (transversely round and thick). On the other hand, comparing a thinner/elliptical/curved beam with the thick, cylindrical beam, the former is expected to have weaker mechanical properties than the latter. Therefore, a decrease in mechanical features is not unexpected as the structure becomes thinner, more elliptical and curved. The increased performance in these fibre features between ‘straight’ and ‘near-straight’ hair is therefore not surprising. The apparent trend of ‘near-straight’ fibres to be thinner than ‘wavy’ fibres is somewhat surprising. Further studies are needed, using a larger sample pool, from interracial ancestry.

Considering the available characterization studies, several data gaps became evident through the described trends. Large intra- and inter-sample variabilities in the observed trends suggest a certain amount of bias slipping in during experimental design, which might be addressed by using finer taxonomies than a race-based or two-point scale (‘straight’, ‘curly’). As noted in [44], experimental design and result interpretation of comparative characterization studies demand at the very least the use of an objective classification scheme. The other data gap, with regard to the previous, is the seeming unawareness of experimental challenges relating to the curved fibre as an interracial or race-independent phenomenon. The argument about bilaterality being a descriptive, rather than a causative, element in curly fibres also highlighted an important data gap. The correlation between bilaterality and fibre curliness seems to be an important fibre feature relationship that supports curvature, but that needs further exploration to unlock the secrets that explain the variabilities in this relationship.

## (b) Why do some fibres curl?

As mentioned above, the ‘why’ question relates mainly to the machinery and processes that produce micro-patterns that are characteristic of the curved fibre, as well as the curved fibre itself. The reason for hair curvature appears to be studied primarily from three viewpoints: anthropology, medicine and biology. Although different in focal points, answers from these perspectives are not necessarily independent, but are often intertwined.

### (i) Anthropology

From an anthropological viewpoint, environmental factors relating to scalp cooling or heat retention form an evolutionary assumption to explain the ‘why’ behind hair curliness [13,71]. Accordingly, the dominating ancient hominid scalp hair form was curly because of the ability of the curved shape to raise the fibre root away from the skin, thereby delivering both UV protection and scalp cooling. Migrating from the hot climate of Africa into colder areas, evolutionary adaptation is thought to have caused changes in hair shape and colour. Sufficient evidence to confirm the hypothesis has not yet been found.

## (ii) Medicine

Besides having a biological interest in the hair fibre as part of fundamental knowledge of the human body, medicine also has a diagnostic interest in asking why hair curls. Changes in intrinsic hair form may be related to a health condition or drug effect. For example, woolly hair may point to certain autosomal recessive hair disorders [72], and changes in hair shape have been observed from treatment of certain conditions (e.g. [3,73]). From a diagnostic perspective, the emphasis of the ‘why’ question pertains to visible features that lead to concern, rather than an interest in the curl phenomenon itself.

## (iii) Biology

*Genetics.* Westgate *et al.* [74] offered a valuable review of the biology and genetics of the curly fibre. From a biological perspective, the ‘why’ question about hair curvature is tackled through investigations of fibre morphogenesis that focus on genetic factors, cellular processes and relevant machinery morphologies that produce a curved shape. In summary, the genetic core and differentiated mechanistic rates govern the follicle morphogenesis. Within this structure, proliferation and differentiation mechanisms drive curly fibre formation and also entrench supportive structures to stabilize and maintain curvature once the fibre protrudes through the scalp. This section begins with a discussion of the genes associated with curvature and then explores other biological theories of curl.

Various genes have been associated with fibre shape, including *TCHH*, *EDAR*, *WNT10A*, *FRAS1*, *OFCC1*, *TRAF2*, *PRSS53*, *PADI3*, *LOC105373470*, *S100A11*, *LCE3E* and *LOC391485* [10,67,75–77]. Of these, a variant of the *EDAR* gene has been indicated (in animal models) to be responsible for straight, coarse, round fibres generated by enlarged follicles [78]. The *EDAR* gene, together with the *TCHH*, gene was confirmed to be present in straight hair from East Asian and European individuals, but not in curly fibres [67,79]. Despite its prominence in straight hair in East Asians, the *EDAR* gene could not explain the variation in hair shape. In addition, the *TCHH* gene appears to play a stronger role in straight hair of Europeans than of East Asians. The *VDR* gene has been identified to be involved in fibre morphogenesis and growth, and therefore may potentially also contribute to fibre shape [80,81]. As more genome-wide association studies explore DNA data, the genetic complexity that contributes to, or governs, fibre shape is bound to provide an improved understanding to the ‘why’ question.

*Follicle machinery and processes.* Activities responsible for fibre formation can loosely be grouped into three categories: namely activities that (i) govern and maintain follicle morphology, (ii) drive fibre formation, and (iii) facilitate structural arrangement and curvature support. The hair follicle (described earlier) is a dynamic structure, developing from the epidermis and dermis downwards, that is subjected to different cycles [24,25]. Of interest to this work is the fully formed hair follicle (described earlier) in the growth (anagen) cycle, which produces a curly hair fibre. The follicle is a much studied structure in medicine and biology (e.g. [25,82–84]), yet it is still not well understood [23]. Detailed activities that govern follicle morphogenesis fall outside the scope of this review.

Follicular pathways, which are thought to account for curvature, are the functioning of certain follicle substructures, differentiated growth rates and molecular expression patterns. A number of theories have been put forward to account for the curvature of a fibre. Based on investigation of biological pathways for molecular bending and twisting, it has been argued that multiple papillary centres form within the DP [85]. As these papillary centres function autonomously, they are likely to generate an asymmetric fibre unless they operate in precise unison. It has also been argued that the fibre is flattened in the DP by certain proliferating mechanisms to produce an elliptical fibre shape [86]. Another theory has suggested that the hardening of the IRS and ORS before fibre formation constrains growth and results in a specific transverse and longitudinal shape [26,85]. Examples of proliferation and differentiation mechanisms that are thought to be causative of fibre curvature are uneven expression of Ki-67 proliferation markers, K14, K38, K82 keratins, transglutaminase-1 enzyme, fibronectin glycoprotein and IGFBP-5 growth

factor [21,31,32]. Metabolites that have been suggested as key to controlling the fibre shape are proteoglycans [87], lipids and exosomes [23]. Since the matrix protein KAP.8.1 is evident in IF packing in OC/PC/MC macrofibrils, it has also been implicated as a causative reason for fibre curvature [59].

As argued before, the cellular arrangement in the cortex and ultrastructural patterns are products of underlying mechanisms. The most prominent study in this regard is detailed in the work of Fraser and Parry [58] and Matsunaga *et al.* [59], which offer theories that explain how IFs align with each other to form MFs, as well as the factors that are likely to govern helical (annular) or hexagonal shapes associated with IF packing in OCs and PCs, respectively. KAPs interact with the embedded KP structures and also strongly influence IF packing during MF formation [52,56]. Hence, they also contribute directly and indirectly to fibre curvature.

#### (iv) Chemical bonding

Owing to popular hair treatments (i.e. cosmetic relaxing and permanent setting), breaking and reformation of disulfide bonds are processes that are closely associated with changes of fibre curliness. As a result, these bonds are believed to cause curvature. However, disulfide bonds are formed during fibre keratinization, a process that occurs after maturation of fully formed cortical cells [25]. As such, the governing elements mentioned earlier have already set the stage for fibre curvature, and the newly formed fibre is equipped (stabilized) in the keratinization zone for extrafollicular existence once it protrudes through the scalp. Disulfide bonds (and other stabilizing cross-links) are therefore probably not directly causative of curvature but, rather, support curvature.

There are still many data gaps when considering the reason for fibre curvature. As aptly described by Bernard [23], ‘much knowledge about hair follicle biology has been acquired in the last 70 years, but the code for molecular and cellular behaviour of the follicle has not yet been broken’. Besides understanding the reason for curvature, the necessity to distinguish between causation and characterization has also been shown, as it introduces confusion in forming comparative causation theories.

#### (c) How do curly fibres behave?

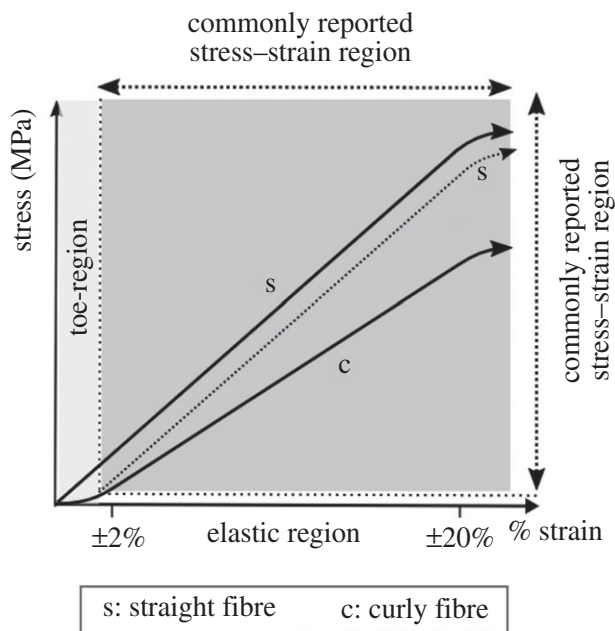
The ‘how’ question is tightly coupled with the ‘what’ question, describing how curly fibres behave under, or respond to, certain conditions. The nature of the ‘how’ question is largely comparative, describing limits and operational ranges of characteristic attributes and also stress-induced deviations from normality. Studies can be categorized loosely into macro- and micro-fibre interests, although these are sometimes combined in an attempt to find important interrelationships between macro- and micro-fibre features. Focusing on the whole structure, diameter, cross-section, lustre, stiffness, rigidity and degree of curliness are typical examples of macroscopic attributes. Microscopic behavioural studies focus on aspects such as biochemical composition, structural arrangement, mechanical properties, growth rate and drug/substance absorption.

##### (i) Physical behaviour

The literature reveals a widespread interest in the fibre’s dimensional (diameter, cross-sectional area, ellipticity) and tensile (elastic limits, break stress load) properties under various conditions (humid, wet, dry, temperature). Besides the interest in dimensional data, they are also required for tensile calculations. A major purpose of tensile studies (usually in mechanical engineering and material and cosmetic sciences) is to find the operational range in which a fibre would maintain its inherent elasticity, without damage or catastrophic failure. Most of these studies appear to have used a race-based taxonomy, comparing the three broad hair types with one another and developing a general trend (despite great intra-variability) about fibre thickness, ellipticity and strength. Accordingly, African (‘curly’) fibres have a low to moderate diameter, longitudinal

polydispersity and elliptical cross-section when compared with European ('near straight') and Asian ('straight') fibres, which are reported to be stronger, thicker, more uniform lengthwise and rounder transversally. African hair is also known to be coarse, except very curly fibres, which are thin. When compared with European fibres, Asian fibres are understood to be slightly thicker and rounder transversally, but have a similar or just slightly higher tensile strength [13,88–90].

As mentioned under the 'what' question, broad trends between fibre diameter, cross-section, curliness and strength have been found in African fibres of different curliness, i.e. an inverse correlation between fibre curliness and strength as well as curliness and diameter [11]. Dimension and tensile strength data for Tunisian females of varying fibre curliness (wavy and curly) also showed the same inverse correlations [91]. However, Tunisian curly fibres were found to be thicker and stronger than curly fibres from African ancestry. A similar study on Mexican females of varying curliness indicated a similar pattern between fibre curliness, dimension and (wet break) strength [92]. From the curl classification of Mexican fibres, it was inferred that Mexican hair corresponded strongly to Asian/European curliness patterns (classes I–IV). It therefore appears that fibre shape, and not ancestry, determines the important correlation between fibre curliness and diameter and between fibre curliness and tensile strength. This observation is confirmed by considering the composition of cystine-rich proteins in the different groups, as these are the dominating contributors to fibre strength. By studying the distribution of cystine-rich proteins under transmission electron microscopy, it has been demonstrated that distribution rates in African fibres are comparable to distribution rates in European and Asian hair [22]. Accordingly, hair weakness in natural, untreated African hair fibres results from excessive structural damage that is consistent with mechanical stress accrued from grooming complex physical structures, and not from structural abnormalities or weaknesses. From an engineering perspective, irrespective of origin, a curved structure presents various physical and mechanical challenges to being groomed. These induce fibre weakening and damage. Tensile evaluation of a weakened structure is likely to yield poor results. However, we have found that current tensile evaluation strategies may be inadequate to determine the tensile strength adequately. We recently reported on incidental observations of distinct toe-region behaviour for curly fibres on the stress–strain plot, which is absent for straight fibres (figure 5) [93]. Accordingly, curly hair fibres exhibit a distinct lag in the toe-region before heeling into elastic deformation, whereas straight hair fibres show immediate elastic responses upon load elongation. Further investigation showed a distinct interrelationship between fibre mechanics and geometry and suggested that the viscoelastic character of hair varies significantly with varying curliness. Showing that fibre curliness is predictable from tensile data, it was pointed out that de facto methods of tensile testing appear to erode curly fibre strength during preparation. Furthermore, de facto tensile strength evaluation methods, based on load elongation at constant rate, largely equate fibre strength with elastic strength, ignoring the viscous contribution of the fibre. The viscous contribution is mostly from the matrix, but, depending on the cuticle size, the cuticle may also contribute to the fibre's viscosity. Reported in [62], the cuticular material may account for 40% of the total fibre weight in fine hair. As mentioned earlier, while African fibres (as an example of curly fibres) are generally known to be coarse, diameter decreases with curliness, which suggests the potential of a larger viscosity contribution from very curly hair than that from medium curly hair. The main outcome of our study indicated that the tensile strength ( $\sigma_T$ ) of hair fibres is composed of two (rather than one main) components, namely a contribution from the toe- as well as the elastic region, namely  $\sigma_T = \sigma_t + \sigma_\epsilon$ , with  $\sigma_t$  and  $\sigma_\epsilon$  signifying the toe- and elastic regions, respectively. Tensile strength of hair fibres is determined as Young's modulus ( $\epsilon$ ), which is the gradient of the elastic region on the stress–strain plot, i.e.  $\epsilon = \sigma/\epsilon$ , where  $\sigma$  and  $\epsilon$  are the stress and strain values, respectively. However, when a viscoelastic material is stretched, tensile strength is represented by a complex ( $\epsilon^*$ ) rather than a simple quantity, i.e.  $\epsilon^* = \epsilon_s + \epsilon_d i$ , where  $\epsilon_s$  is the material's elastic stiffness and  $\epsilon_d$  is the fibre's energy dissipative ability observed as a result of viscous damping [94]; this agrees with our findings, namely that  $\sigma_T = \epsilon_t \epsilon + \epsilon_\epsilon \epsilon$ , rather than  $\sigma_T = \epsilon_\epsilon \epsilon$ . While both toe- and elastic regions have an elastic and a viscosity contribution, the elastic contribution dominates in the elastic region, whereas the viscosity contribution dominates in the toe-region. For non-curly



**Figure 5.** Stress–strain plot for straight and curly hair fibres. For curly hair fibres, there exists a toe-region prior to the linear elastic region.

fibres, the greatest part of fibre strength is derived from  $\sigma_e$  while  $\sigma_t \approx 0$ . For curly fibres,  $\sigma_t$  adds significantly to the overall strength, even though  $\sigma_e$  remains the major contributor.

## (ii) Absorption behaviour

Another commonly studied behaviour is the fibre's response to external or internal chemical exposure. Structural responses to external exposure mostly pertain to cosmetic treatments and, to a lesser extent, photo-oxidative exposure or environmental exposure. External absorption response interests lie in understanding the kinetics and mechanisms of the exposure; the structural and ultrastructural changes (damages) due to the exposure; the impact on hair strength and surface properties; and also strategies to improve the condition of damaged hair (e.g. [13, 95–99]). Owing to consumer popularity of using chemical relaxing and grey-covering treatment on the hair, these topics remain important and are likely to be re-investigated frequently with the emergence of improved instruments/techniques or chemical treatments applied to the hair (e.g. [100,101]). Shown by Coderch *et al.* [40,102], a modification of the Guggenheim–Anderson–Boer sorption model (initially for soil water vapour sorption isotherms) is well suited to evaluate the changes in the permeation characteristics of the hair fibres. Accordingly, the sorbed moisture content ( $M$  in g/100 g) at water activity  $a_w$  can be monitored by  $M = M_1 c K a_w / (1 - K a_w + c K a_w)$ , where  $M_1$  is the sorbed monolayer moisture content (in g/100 g) and  $c$  and  $K$  are energy constants depicting the difference in free enthalpy of the water molecules in the pure liquid state and in the monolayer (in the case of  $c$ ) or in the upper layers in the case of ( $K$ ).

Forensic, medicinal and pharmacological sciences are generally more interested in internal, rather than external, exposure of the fibre to chemicals, although forensic investigations have some interest in exogenous influences. Chemical deposition via endogenous absorption of substances facilitates a non-invasive means to trace chemicals to which the individual was exposed, long after pathological evidence of exposure. This method is not without its challenges. Endogenous absorption is affected by chemical treatments (permanent and semi-permanent) of the hair, which have been found to markedly alter the content of certain drug markers

used for hair analyses [103]. False positives for substance abuse are often reported in forensic investigations. In the USA, there appears to be a higher positive rate for drugs in African (assumed curly) than in European hair (assumed near straight). The view that the elevated rate is attributable to ancestry has recently been challenged [104]. Accordingly, certain types of cosmetic products ('ethnic hair care') increase diffusivity of hair. Applying the same products on hair from African and European ancestry, absorption susceptibility of all fibres was found to increase, which, in turn, resulted in similar drug uptake rates irrespective of race.

Absorption of chemical substances (in any medium) is strongly affected by the hydrophilicity/lipophilicity, pH and other substances in the absorbing medium. As mentioned, there is race-independent direct correlation between fibre shape and cortical cell composition [56,64], and the chemical composition between PCs and OCs differs [64,65]. Furthermore, to the best of our knowledge, there are no reported data on lipid distribution in different hair forms, only race-based lipid distribution reports [17,18,43]. A group of Spanish researchers investigating lipid contents in various hair types [18,40,102] has reported (among many findings) that African hair has the greatest amount of exogenous lipids with lower permeability than European and Asian hair. It was shown that, after depletion of exogenous lipids, absorption kinetics remained constant, but desorption kinetics changed, leading to a loss of total moisture content. On the other hand, depletion of endogenous lipids promoted lower water permeability. The European and Asian hair used in the mentioned Spanish studies [18,40,102] appears to be straight, or almost straight. Furthermore, fibres were acquired commercially, and there is no indication of the size of the donor sample pools from the reported literature. It is therefore impossible to determine whether these important findings are generally true for specific racial groups, or whether they are phenotypical. A recent study [105] by the same group, where different colour hair from the same racial group was subjected to similar investigations, seems to point to a phenotypical rather than racial origin. Results showed a significant difference in cuticle lipid content, as well as different absorption/desorption dynamics between the white and brown hair. White fibres exhibited decreased absorption capacity and increased rate of permeability. This raises a question about how these observations would differ between fibres of different curliness in the same population. Considering that certain fibre features, previously attributed to race, were later found to be attributable to fibre shape, there is a strong likelihood that lipid distribution may have a phenotypical, rather than racial, nature. If true, it would not be irrational to suggest dissimilarities in biochemical environment (among curly and non-curly fibres) that would affect absorption. This would be critical for correct data interpretations, especially in medicine, pharmacology, forensics and toxicology.

### (iii) Surface properties

Various studies characterize and compare mechanical surface properties of the fibre. Typical surface properties include fibre lustre (versus dullness), fractures in the surface (lack of smoothness, increased friction coefficient and tangling due to damage), hardness (bending stiffness and torsional rigidity), etc. [13,16,106–108]. Theory suggests that surface properties of curly structures are likely to be dissimilar to those of straight structures. Not many studies could be found for surface properties of curly fibres *per se*. However, when compared with European/Asian fibres, fibres from African ancestry have a higher friction coefficient, less lustre, higher torsional rigidity and show more surface damage in general [13–15].

### (iv) Growth behaviour

Growth rates of fibres are sometimes also studied in a comparative fashion. A 2012 study [109] of fibres of low curvature is worth mentioning as it provides a comparative tool to understand curly fibres. The sample pool consisted of straight hair (STAM classes I and II) from East Asian ( $n = 26$ ) and European ( $n = 6$ ) donors, from which more than 1000 hair fibres were evaluated. By focusing on the relationships between growth rate and certain morphological parameters, it was found that thicker hair corresponds to faster growth rates, a higher probability of having a medulla and

shorter interscale distances, whereas the opposite was demonstrated for slower growing fibres. A significant conclusion of the study was that findings on growth rates of East Asian and European fibres were independent from ancestry but dependent on certain fibre characteristics. In an earlier related study [110], an opposite inference was made, namely that growth rates corresponded to race: African < European < Asian. While the earlier study evaluated a larger sample pool (511 donors), ancestry was the differentiator and not fibre characteristics.

The 'how' question highlighted that some comparative studies are pointing towards phenotypical curly fibre trends that are independent of race. It also showed that it is clear that a race-based taxonomy, without at least accounting for different curl types, leads to confounding effects. The 'how' question, again, highlights the need for large-scale studies based on phenotypical taxonomies in order to better understand and describe fibre behaviour under various conditions.

### 3. Conclusion on review of current research

Significant effort has been directed towards understanding why fibres curl, characterizing the macro- and micro-appearances (characters) of the curly fibre and determining how the curly fibre is likely to behave under different conditions. Three main observations have been made from the review: (i) the curly fibre appears to be a distinct type of fibre, with its own physical, mechanical and biological make-up; (ii) using a race-based taxonomy introduces complexity and bias to understanding the curly fibre, which hinders the recognition of phenotypical trends; and (iii) uncritical use of terminology, such as 'European' and 'Caucasian' hair or 'African' and 'ethnic' or 'afro' hair, escalates the problems made in the previous points. It also thwarts objective comparison of relevant studies. An appropriate guiding question for future hair research may be to ask how much of the 'why', 'what' and 'how' is ascribable to genotype and how much to the phenotype.

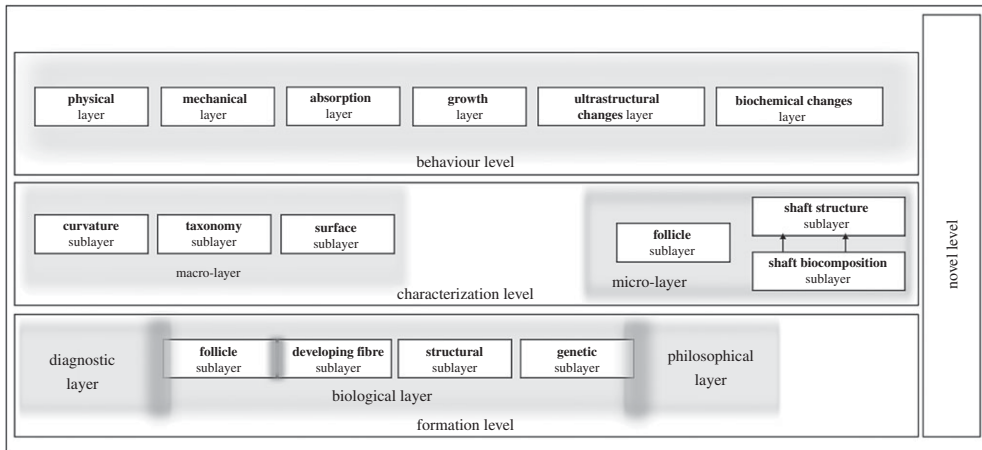
From a sizeable DNA hair phenotyping study [10], it appears that more than 50% of hair fibres from European, African, Asian (including Middle, Eastern and Western) and admixed populations exhibit some degree of curl. The high incidence of fibre curvature points to the 'ordinariness' (rather than peculiarity) that curly fibres should enjoy when studying hair. If most advances in hair research in the past were made based on available straight/near-straight hair sample pools, the current presentation of fibre development, growth, character and behaviour (mostly from the perspective of straight fibre) is logical. However, were these initial sample pools mostly curly, the fundamental view on hair would have been coloured differently and the narrative would read as follows: Hair comprises many scalp-protruding fibres that adopt a variety of curved shapes. A fibre is formed in a curved follicle, which is embedded in the scalp, at a gradient. The shape of the follicle is geared towards producing a curved structure, having an asymmetric distribution of follicular substructures and certain follicular substances. In cases where the fibre develops without a curved shape, the follicle may be expected to be at right angles to the scalp and without the asymmetry that is needed for shape formation. In these instances, the growing fibre adopts a round (as opposed to an elliptical) transverse shape, and is potentially thicker than normal. Without the mechanical limitations of curvature, these fibres are also likely to have higher elastic limits.

### 4. A systemized approach to curly hair investigations

#### (a) Curvature fibre model

Based on the discussion presented in the review section, it is evident that a framework for considering curly hair research would be beneficial. To this end, a curvature fibre model is presented in this section. The main purpose of this model is to present a systemized architecture of curly fibre elements. It is important to note that the design of the curvature fibre model is





**Figure 6.** The curvature model enables easier categorization of research activities relating to curly hair fibres.

based on historic and current research interests that focus on hair shape. The review and model are therefore only a subset of general hair fibre research. The model described below might be extended to all types of hair research, but, for such a purpose, the above review would need comprehensive expansion. In its current form, extension of the curvature fibre model would be required as new relevant research topics arise.

Extrapolated from the broad focal points of relevant research activities, the model architecture exists as three main tiers, namely the formation (why), characterization (what) and behaviour (how) levels. A fourth tier, the novel level, exists alongside other levels and leaves a vacancy for new topics relating to curly hair research (figure 6).

### (i) Formation level

The formation level explains why certain fibres are curved. The level comprises three lateral layers, namely the biological, philosophical and diagnostic layers. In the biological layer, which we focus on, four sublayers summarize the main activities that explain the causation of curvature. These include the follicle sublayer that accounts for research activities on follicle morphogenesis. Closely related, and often intertwined with the follicle sublayer, is the developing fibre sublayer, where proliferation and differentiation activities that give rise to the fibre's shape are explored. Theories that describe mechanisms that form specific structures (e.g. IFs and MFs) supporting fibre curvature belong to the structural sublayer of the biological layer. It must be noted at this point that structural sublayers of the biological layer (in the formation level) and micro-layer (in the characterization level) are likely to share a high level of commonality. Level distinction is made by asking whether the research activity describes an observed phenomenon, or whether it describes a process/activity. Studies that report on the visual appearance of patterns or structures (e.g. via various microscopic techniques) are micro-characterization activities. On the other hand, research theories that describe mechanistic processes that lead to specific visual appearances of patterns or structures are assigned to the formation level, as they offer explanations of why fibres curl.

Anthropological and palaeontological theories of why fibres curl belong to the philosophical layer. Both of these two sciences often cooperate with biological sciences. Therefore, interaction between the philosophical and biological layers, especially the genetic sublayer, is expected. The diagnostic layer, which is mostly concerned with health or drug effects that cause otherwise straight hair to curl, is also likely to interact with the biological layer. In this case, interaction is mostly expected to be with the follicle and developing fibre sublayers, where the developing fibre is exposed to disease or drugs from the bloodstream.

## (ii) Characterization level

The characterization level describes the visual appearance of the fibre, which may be plainly observable or may require micro-investigations (e.g. microscopy, spectroscopy and chemical analysis). Macro-characterization research activities describe not only visible fibre traits but also development of tools, terminology and classes to accurately depict the curly fibre. These activities belong to the curvature, taxonomy and surface sublayers, respectively. For the curvature sublayer, research activities focus on developing and using appropriate geometric descriptors (e.g. curvature degree, index, width, depth and amplitude) for various applications. The taxonomy sublayer hosts research activities that develop and describe taxonomies, which classify fibres in order to support further (other) fibre investigations. Various visual/surface characteristics of the fibre (e.g. lustre, diameter and stiffness) are studied in the surface sublayer.

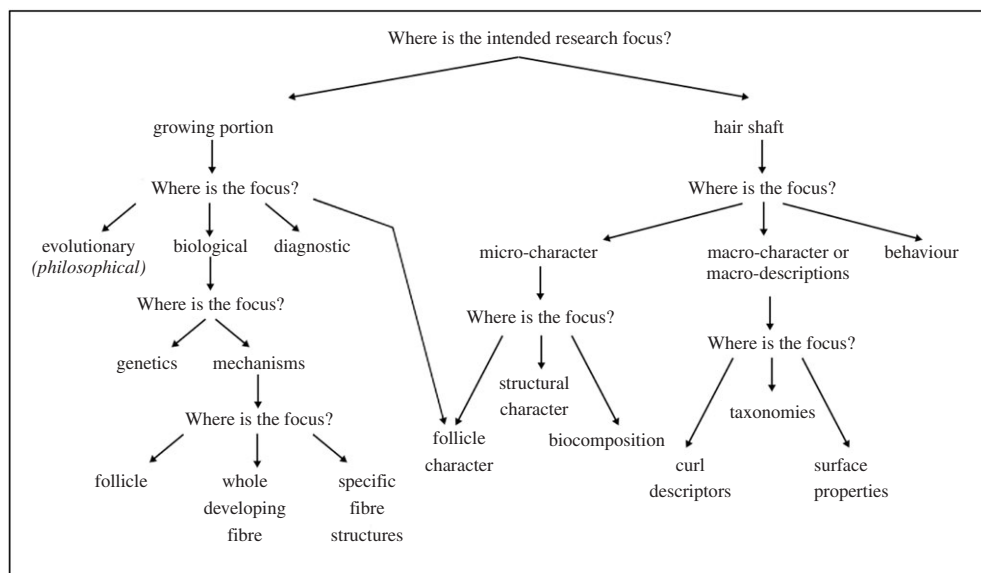
Micro-characterization of curvature focuses on the follicle, structural units of the shaft, their interrelationships and multidimensional interactions. As such, micro-layer characterization is categorized in the follicle, shaft structure and shaft biocomposition sublayers. Micro-shaft structures are formed and supported by biochemical components, comprising proteins, lipids, water and other cellular material. The two shaft sublayers are consecutive in nature, with the biocomposition having a regulating effect on the formed structures. The shaft biocomposition describes not only relevant biomolecules but also the chemical bonds that drive underlying bonding networks, which are pivotal in fibre curvature.

## (iii) Behaviour level

Fibre behaviour studies may have a characterization or comparative nature. In the first instance, fibre behaviour studies are used to determine how a curly fibre would deviate from its normal character under certain (usually stress) conditions. Monitoring the behaviour of the fibre, pre-selected fibre properties are characterized, e.g. application of mechanical stress is used to characterize the fibre's material strength, bending and torsional properties. Behaviour studies with a comparative nature aim at establishing performance ranges of specific types of fibres. For example, how does the tensile strength of curly hair compare with that of non-curly hair? Currently, most of the comparative studies use different populations or races, and not degree of curliness, as the comparison discriminant. Distinguishable behavioural layers or classes include the physical, mechanical, absorption, growth, ultrastructural changes and biochemical changes layers. The physical layer describes the behaviour(s) of the fibre surface under various test conditions; the mechanical layer is a platform where mechanical responses of the fibre to various test conditions are described/compared; research activities on the absorption layer investigate endogenous and exogenous absorption of the fibre. Depending on the interests of the specific discipline, the absorption responses may be intertwined with any of the other layers on the behaviour level. For example, forensic and medical scientists may be interested in the biochemical changes of the fibre, while engineering sciences may be interested in mechanical and ultrastructural changes after fibre absorption. The growth layer provides a platform for positive and negative growth rate studies. Currently, growth rate studies that relate to curly fibres are mostly comparative in nature. Furthermore, current comparative studies seem to use population/race as a comparison discriminant, and not degree of curliness. Negative growth rates (hair loss) do not appear to be studied from the perspective of curly fibres as a distinct phenotype. The final two layers on the behaviour level provide a platform to describe how the fibre changes microscopically after being subjected to certain stresses or environments.

## (b) Application of the curvature fibre model to human scalp hair

The described model presents a simplistic interpretation of current research topics on curly hair. Application of the curvature fibre model (with references to case literature) is depicted in figure 7. As a first research step, applicable literature reviews typically guide experimental planning or theory development. It is at this point that researchers may spend a significant amount of



**Figure 7.** Application of the curvature fibre model.

time trying to make sense of the myriad of hair research material, with efforts that may be marked by an inverse correlation between frustration and productivity. Being able to distinguish between apples and pears in publications that intersperse them may be challenging, especially for younger researchers.

Using the model to converge literature searches, it is necessary to ask whether intended research focuses on the growing portion of the fibre or on the hair shaft protruding through the scalp. Based on the answer, further questions are asked. If intended research focus is on the growing portion, does the intended research concentrate on biological, evolutionary or diagnostic reasons of why hair curls? If not, the research probably belongs to the characterization layer. If the answer is affirmative, it is necessary to determine in which of the three focus areas the research would reside: biological, evolutionary or diagnostic. In case the research has a biological nature, further decision-making is necessary, namely whether it has a genetic or mechanistic nature. If mechanistic, the main focus area (follicle, developing (whole) fibre or specific fibre structures) of the mechanisms to be studied must be established.

If the study intends to characterize the follicle, it would belong to the follicle sublayer in the micro-layer of the characterization level. However, if it were to concentrate on characterizing the hair shaft rather than the follicle, the first question to ask is whether the research focuses on macro- (surface) or micro-features of the fibre. Surface-based research activities may be handles (classification or terminology) to better describe curvature or may be physical properties such as fibre dimension, colour, tangling, interscale cuticle distances and so on. Micro-characterizations focus either on the follicle or on the shaft. Follicle characterization studies commonly interweave structural and biochemical observations, whereas these topics are often separated in shaft characterization studies.

To establish whether or not the intended research would study the behaviour of the fibre, it is necessary to ask whether the intention is to study certain fibre properties under stress or extraordinary conditions. Alternatively, intended research may want to compare fibres from different sample pools with one another. If the answer is yes to either of these questions, the final step is to pigeonhole the intended research as physical, mechanical, absorption, growth, ultrastructural or biochemical related. If the answer is no to the former two questions, the intended research is likely to be a novel topic. In this case, extension of the model would be in the interest of the body of knowledge relating to curly fibres.

## 5. Conclusion

The paper presented a literature review on research of curly scalp fibres. The review categorized existing research areas into three categories, essentially asking why fibres curl, what the curly fibre looks like and how the curly fibre behaves. Several data gaps also became evident, of which the most important was that the use of race-based taxonomies in curly fibre research introduces complexity and bias to understanding the curly fibre as a phenotype, which, in turn, hinders the recognition of phenotypical trends. Based on the review, we also presented a first effort to systematize research activities on fibre curvature into a usable model. The model gives an instant overview of relevant available research focus areas. Supplied guidelines for applying the model during research planning are expected to help clarify the intended research focus among the myriad of topical research interests; assist in performing targeted literature searches; assist with comparative studies (comparing apples with apples); and help highlight areas in which more research is required.

**Data accessibility.** This article has no additional data.

**Authors' contributions.** E.C. wrote the paper. M.N.N. and N.P.K. edited the manuscript.

**Competing interests.** We declare we have no competing interests.

**Funding.** Funding for this work was received from the National Research Foundation SARChI Chair for Dermatology and Toxicology and The South African Medical Research Council.

## References

1. Park JH, Park JM, Kim NR, Manonukul K. 2017 Hair diameter evaluation in different regions of the safe donor area in Asian populations. *Int. J. Dermatol.* **56**, 784–787. (doi:10.1111/ijd.13638)
2. Xiang L, Sunesara I, Rehm KE, Marshall Jr GD. 2016 Hair cortisol concentrations are associated with hair growth rate. *Neuroimmunomodulation* **23**, 287–294. (doi:10.1159/000455867)
3. Keating M, Dasanu CA. 2017 Late-onset robust curly hair growth in a patient with BRAF-mutated metastatic melanoma responding to dabrafenib. *J. Oncol. Pharm. Pract.* **23**, 309–312. (doi:10.1177/1078155216635854)
4. Ocampo-Garza J, Tosti A. 2019 Trichoscopy of dark scalp. *Ski Appendage Disord.* **5**, 1–8. (doi:10.1159/000488885)
5. Trueb R, Henry J, Davis M, Schwartz J. 2018 Scalp condition impacts hair growth and retention via oxidative stress. *Int. J. Trichol.* **10**, 262–270. (doi:10.4103/ijt.ijt\_57\_18)
6. Fabbrocini G, Cantelli M, Masarà A, Annunziata MC, Marasca C, Cacciapuoti S. 2018 Female pattern hair loss: a clinical, pathophysiologic, and therapeutic review. *Int. J. Women's Dermatol.* **4**, 203–211. (doi:10.1016/j.ijwd.2018.05.001)
7. Kunchi C, Venkateshan K, Adusumalli R. 2018 Effect of scalp position on tensile properties of single hair fibers. *Int. J. Trichol.* **10**, 218–228. (doi:10.4103/ijt.ijt\_19\_18)
8. Kunchi C, Venkateshan K, Reddy N, Adusumalli R. 2018 Correlation between mechanical and thermal properties of human hair. *Int. J. Trichol.* **10**, 204–210. (doi:10.4103/ijt.ijt\_24\_18)
9. Cloete E, Khumalo NP, Van Wyk JC, Ngoepe MN. 2019 Systems approach to human hair fibers: interdependence between physical, mechanical, biochemical and geometric properties of natural healthy hair. *Front. Physiol.* **10**, 112. (doi:10.3389/fphys.2019.00112)
10. Pośpiech E *et al.* 2018 Towards broadening forensic DNA phenotyping beyond pigmentation: improving the prediction of head hair shape from DNA. *Forensic Sci. Int. Genet.* **37**, 241–251. (doi:10.1016/j.fsigen.2018.08.017)
11. Porter CE, Dixon F, Khine C-C, Pistorio B, Bryant H, de la Mettrie R. 2009 The behavior of hair from different countries. *J. Cosmet. Sci.* **60**, 97–109. (doi:10.1111/j.1468-2494.2010.00534\_2.x)
12. Lasisi T, Ito S, Wakamatsu K, Shaw CN. 2016 Quantifying variation in human scalp hair fiber shape and pigmentation. *Am. J. Phys. Anthropol.* **160**, 341–352. (doi:10.1002/ajpa.22971)
13. Robbins CR. 2012 *Chemical and physical behavior of human hair*, p. 746. Berlin, Germany: Springer.
14. Bhushan B. 2010 *Biophysics of human hair: structural, nanomechanical, and nanotribological studies*, p. 192. Berlin, Germany: Springer.

15. Khumalo NP, Doe PT, Dawber RPR, Ferguson DJP. 2000 What is normal black African hair? A light and scanning electron-microscopic study. *J. Am. Acad. Dermatol.* **43**, 814–820. (doi:10.1067/mjd.2000.107958)
16. Wortmann F-J, Schwan-Jonczyk A. 2006 Investigating hair properties relevant for hair 'handle'. Part I: hair diameter, bending and frictional properties. *Int. J. Cosmet. Sci.* **28**, 61–68. (doi:10.1111/j.1467-2494.2006.00306.x)
17. Cruz CF *et al.* 2013 Keratins and lipids in ethnic hair. *Int. J. Cosmet. Sci.* **35**, 244–249. (doi:10.1111/ics.12035)
18. Martí M, Barba C, Manich AM, Rubio L, Alonso C, Coderch L. 2016 The influence of hair lipids in ethnic hair properties. *Int. J. Cosmet. Sci.* **38**, 77–84. (doi:10.1111/ics.12261)
19. Hrdy D. 1973 Quantitative hair form variation in seven populations. *Am. J. Phys. Anthropol.* **39**, 7–18. (doi:10.1002/ajpa.1330390103)
20. de la Mettrie R, Saint-Léger D, Loussouarn G, Garcel A-L, Porter C, Langaney A. 2007 Shape variability and classification of human hair: a worldwide approach. *Hum. Biol.* **79**, 265–281. (doi:10.1353/hub.2007.0045)
21. Thibaut S, Barbarat P, Leroy F, Bernard BA. 2007 Human hair keratin network and curvature. *Int. J. Dermatol.* **46**, 7–10. (doi:10.1111/j.1365-4632.2007.03454.x)
22. Khumalo NP, Dawber RPR, Ferguson DJP. 2005 Apparent fragility of African hair is unrelated to the cystine-rich protein distribution: a cytochemical electron microscopic study. *Exp. Dermatol.* **14**, 311–314. (doi:10.1111/j.0906-6705.2005.00288.x)
23. Bernard BA. 2017 The hair follicle enigma. *Exp. Dermatol.* **26**, 472–477. (doi:10.1111/exd.13337)
24. Bernard BA. 2003 Hair shape of curly hair. *J. Am. Acad. Dermatol.* **48**, S120–S126. (doi:10.1067/mjd.2003.279)
25. Rogers GE. 2004 Hair follicle differentiation and regulation. *Int. J. Dev. Biol.* **48**, 163–170. (doi:10.1387/ijdb.15272381)
26. Birngruber CG, Verhoff MA. 2012 The color of human hair. In *Handbook of hair in health and disease* (ed. VR Preedy), p. 477. Wageningen, The Netherlands: Academic Publishers.
27. Ohshima M. 2007 Hair follicle bulge: a fascinating reservoir of epithelial stem cells. *J. Dermatol. Sci.* **46**, 81–89. (doi:10.1016/j.jdermsci.2006.12.002)
28. Veijouye SJ, Yari A, Heidari F, Sajedi N, Moghani FG, Nobakht M. 2017 Bulge region as a putative hair follicle stem cells niche: a brief review. *Iran J. Public Health* **46**, 1167–1175.
29. Stuart TP. 1882 The curled hair and curved hair follicle of the negro. *J. Anat. Physiol.* **16**, 362–363.
30. Lindelöf B, Forslind B, Hedblad M-A. 1988 Human hair form. *Arch. Dermatol.* **124**, 1359. (doi:10.1001/archderm.1988.01670090015003)
31. Thibaut S, Gaillard O, Bouhanna P, Cannell DW, Bernard BA. 2005 Human hair shape is programmed from the bulb. *Br. J. Dermatol.* **152**, 632–638. (doi:10.1111/j.1365-2133.2005.06521.x)
32. Sriwiriyanont P *et al.* 2011 Effects of IGF-binding protein 5 in dysregulating the shape of human hair. *J. Invest. Dermatol.* **131**, 320–328. (doi:10.1038/jid.2010.309)
33. Swift JA, Bews B. 1974 The chemistry of human hair cuticle-II: the isolation and amino acid analysis of the cell membranes and A-layer. *J. Soc. Cosmet. Chem.* **25**, 355–366.
34. Swift JA, Bews B. 1976 The chemistry of human hair cuticle—III: the isolation and amino acid analysis of various subfractions of the cuticle obtained by pronase and trypsin digestion. *J. Soc. Cosmet. Chem.* **27**, 289–300.
35. Swift JA. 1999 Human hair cuticle: biologically conspired to the owner's advantage. *J. Soc. Cosmet. Chem.* **50**, 23–47.
36. Levitt M, Chothia C. 1976 Structural patterns in globular proteins. *Nature* **261**, 552–558. (doi:10.1038/261552a0)
37. Richardson JS. 1981 The anatomy and taxonomy of protein structure. *Adv. Protein Chem.* **34**, 167–339. (doi:10.1016/S0065-3233(08)60520-3)
38. Banerjee AR. 1965 Variations in the medullary structure of human head hair. *Z. Morphol. Anthropol. Bd H.* **57**, 56–69.
39. Masukawa Y, Narita H, Imokawa G. 2005 Characterization of the lipid composition at the proximal root regions of human hair. *J. Cosmet. Sci.* **56**, 1–16. (doi:10.1111/j.0142-5463.2005.00265\_1.x)
40. Coderch L, Oliver MA, Martínez V, Manich AM, Rubio L, Martí M. 2017 Exogenous and endogenous lipids of human hair. *Skin Res. Technol.* **23**, 479–485. (doi:10.1111/srt.12359)

41. Robbins C. 2009 The cell membrane complex: three related but different cellular cohesion components of mammalian hair fibers. *J. Cosmet. Sci.* **60**, 437–465.
42. Liu H, Bryson WG. 2002 A three-component model of the wool fibre—effects of morphology, elasticity and intermediate filament arrangement on fibre stiffness. *J. Text. Inst.* **93**, 121–131. (doi:10.1080/00405000208630557)
43. Ji JH, Park T-S, Lee H-J, Kim Y-D, Pi L-Q, Jin X-H, Lee W-S. 2013 The ethnic differences of the damage of hair and integral hair lipid after ultra violet radiation. *Ann. Dermatol.* **25**, 54. (doi:10.5021/ad.2013.25.1.54)
44. Maneli MH, Mkentane K, Khumalo NP. 2013 Lipid distribution and influence on hair structure. *Int. J. Cosmet. Sci.* **35**, 523–523. (doi:10.1111/ics.12070)
45. Feughelman M. 2016 A model for the mechanical properties of the  $\alpha$ -keratin cortex. See <http://dx.doi.org/10.1177/004051759406400408>.
46. Hearle JW. 2000 A critical review of the structural mechanics of wool and hair fibres. *Int. J. Biol. Macromol.* **27**, 123–138. (doi:10.1016/S0141-8130(00)00116-1)
47. Kadir M, Wang X, Zhu B, Liu J, Harland D, Popescu C. 2017 The structure of the ‘amorphous’ matrix of keratins. *J. Struct. Biol.* **198**, 116–123. (doi:10.1016/j.jsb.2017.04.001)
48. Harland DP, Walls RJ, Vernon JA, Dyer JM, Woods JL, Bell F. 2014 Three-dimensional architecture of macrofibrils in the human scalp hair cortex. *J. Struct. Biol.* **185**, 397–404. (doi:10.1016/j.jsb.2014.01.010)
49. Wang B, Yang W, McKittrick J, Meyers MA. 2016 Keratin: structure, mechanical properties, occurrence in biological organisms, and efforts at bioinspiration. *Prog. Mater. Sci.* **76**, 229–318. (doi:10.1016/j.pmatsci.2015.06.001)
50. Thomas A *et al.* 2012 Interspecies comparison of morphology, ultrastructure, and proteome of mammalian keratin fibers of similar diameter. *J. Agric. Food Chem.* **60**, 2434–2446. (doi:10.1021/jf204811v)
51. Wortmann FJ, Wortmann G. 2018 A somewhat unexpected result from the deconvolution of DSC curves for human hair: there is no apparent relation between cortical cell fractions and hair curliness. *Exp. Dermatol.* **27**, 292–294. (doi:10.1111/exd.13462)
52. Bryson WG, Harland DP, Caldwell JP, Vernon JA, Walls RJ, Woods JL, Nagase S, Itou T, Koike K. 2009 Cortical cell types and intermediate filament arrangements correlate with fiber curvature in Japanese human hair. *J. Struct. Biol.* **166**, 46–58. (doi:10.1016/j.jsb.2008.12.006)
53. Nagase S *et al.* 2008 Characterization of curved hair of Japanese women with reference to internal structures and amino acid composition. *J. Cosmet. Sci.* **59**, 317–332.
54. Plowman J, Paton L, Bryson W. 2007 The differential expression of proteins in the cortical cells of wool and hair fibres. *Exp. Dermatol.* **16**, 707–714. (doi:10.1111/j.1600-0625.2007.00576.x)
55. Harland DP *et al.* 2018 Intrinsic curvature in wool fibres is determined by the relative length of orthocortical and paracortical cells. *J. Exp. Biol.* **221**, jeb172312. (doi:10.1242/jeb.172312)
56. Orwin DFG, Woods JL, Ranford SL. 1984 Cortical cell types and their distribution in wool fibres. *Aust. J. Biol. Sci.* **37**, 237–255. (doi:10.1071/BI9840237)
57. Kaplin IJ, Whiteley KJ. 1978 An electron microscope study of fibril : matrix arrangements in high-and low-crimp wool fibres. *Aust. J. Biol. Sci.* **31**, 231–240. (doi:10.1071/bi9780231)
58. Fraser RDB, Parry DAD. 2018 Structural hierarchy of trichocyte keratin intermediate filaments. In *The hair fibre: proteins, structure and development* (eds JE Plowman, DP Harland, S Deb-Choudhury), pp. 57–70. Singapore: Springer.
59. Matsunaga R, Abe R, Ishii D, Watanabe S, Kiyoshi M, Nöcker B, Tsuchiya M, Tsumoto K. 2013 Bidirectional binding property of high glycine–tyrosine keratin-associated protein contributes to the mechanical strength and shape of hair. *J. Struct. Biol.* **183**, 484–494. (doi:10.1016/j.jsb.2013.06.005)
60. Rogers GE, Powell BC. 1993 Organization and expression of hair follicle genes. *J. Invest. Dermatol.* **101**(Suppl. 1), 50S–55S. (doi:10.1111/1523-1747.ep12362626)
61. Jenkins BJ, Powell BC. 1994 Differential expression of genes encoding a cysteine-rich keratin family in the hair cuticle. *J. Invest. Dermatol.* **103**, 310–317. (doi:10.1111/1523-1747.ep12394770)
62. Wolfram LJ, Lindemann MKO. 1971 Some observations on the hair cuticle. *J. Soc. Cosmet. Chem.* **22**, 839–850.
63. Crewther WG, Gillespie JM, Harrap BS, Inglis AS. 1966 Low-sulfur proteins from  $\alpha$ -keratins. Interrelationships between their amino acid compositions,  $\alpha$ -helix

- contents, and the supercontraction of the parent keratin. *Biopolymers* **4**, 905–916. (doi:10.1002/bip.1966.360040807)
64. Plowman JE, Deb-Choudhury S, Bryson WG, Clerens S, Dyer JM. 2009 Protein expression in orthocortical and paracortical cells of merino wool fibers. *J. Agric. Food Chem.* **57**, 2174–2180. (doi:10.1021/jf803290h)
  65. Kulkarni VG, Bradbury JH. 1974 The chemical composition of wool. XII Further studies on cortical cells and macrofibrils. *Aust. J. Biol. Sci.* **27**, 383–396. (doi:10.1071/B19740383)
  66. Adhikari K *et al.* 2016 A genome-wide association scan in admixed Latin Americans identifies loci influencing facial and scalp hair features. *Nat. Commun.* **7**, 10815. (doi:10.1038/ncomms10815)
  67. Pośpiech E *et al.* 2018 Variation in the RPTN gene may facilitate straight hair formation in Europeans and East Asians. *J. Dermatol. Sci.* **91**, 331–334. (doi:10.1016/j.jdermsci.2018.06.003)
  68. Mkentane K, Van Wyk JC, Sishi N, Gumedze F, Ngoepe M, Davids LM, Khumalo NP. 2017 Geometric classification of scalp hair for valid drug testing, 6 more reliable than 8 hair curl groups. *PLoS ONE* **12**, e0172834. (doi:10.1371/journal.pone.0172834)
  69. Eriksson N *et al.* 2010 Web-based, participant-driven studies yield novel genetic associations for common traits. *PLoS Genet.* **6**, e1000993. (doi:10.1371/journal.pgen.1000993)
  70. Bouabbache S, Galliano A, Littaye P, Leportier M, Pouradier F, Gillot E, Panhard S, Lousouarn G. 2016 What is a Caucasian ‘fine’ hair? Comparing instrumental measurements, self-perceptions and assessments from hair experts. *Int. J. Cosmet. Sci.* **38**, 581–588. (doi:10.1111/ics.12323)
  71. Jablonski NG. 2006 *Skin: a natural history*, p. 281. Berkeley, CA: University of California Press.
  72. Duverger O, Morasso MI. 2014 To grow or not to grow: hair morphogenesis and human genetic hair disorders. *Semin. Cell Dev. Biol.* **25–26**, 22–33. (doi:10.1016/j.semcd.2013.12.006)
  73. Choe SJ, Kim BJ, Choi J, Lee WS. 2017 Acquired hair curling after diphenylcyclopropanone immunotherapy in alopecia areata patient. *J. Eur. Acad. Dermatol. Venereol.* **31**, e371–e372. (doi:10.1111/jdv.14169)
  74. Westgate GE, Ginger RS, Green MR. 2017 The biology and genetics of curly hair. *Exp. Dermatol.* **26**, 483–490. (doi:10.1111/exd.13347)
  75. Pośpiech E *et al.* 2015 Evaluation of the predictive capacity of DNA variants associated with straight hair in Europeans. *Forensic Sci. Int. Genet.* **19**, 280–288. (doi:10.1016/j.fsigen.2015.09.004)
  76. Liu F *et al.* 2018 Meta-analysis of genome-wide association studies identifies 8 novel loci involved in shape variation of human head hair. *Hum. Mol. Genet.* **27**, 559–575. (doi:10.1093/hmg/ddx416)
  77. Wu S *et al.* 2016 Genome-wide scans reveal variants at EDAR predominantly affecting hair straightness in Han Chinese and Uyghur populations. *Hum. Genet.* **135**, 1279–1286. (doi:10.1007/s00439-016-1718-y)
  78. Mou C, Thomason HA, Willan PM, Clowes C, Harris WE, Drew CF, Dixon J, Dixon MJ, Headon DJ. 2008 Enhanced ectodysplasin-A receptor (EDAR) signaling alters multiple fiber characteristics to produce the East Asian hair form. *Hum. Mutat.* **29**, 1405–1411. (doi:10.1002/humu.20795)
  79. Bryk J, Hardouin E, Pugach I, Hughes D, Strotmann R, Stoneking M, Myles S. 2008 Positive selection in East Asians for an EDAR allele that enhances NF- $\kappa$ B activation. *PLoS ONE* **3**, e2209. (doi:10.1371/journal.pone.0002209)
  80. Palmer HG, Anjos-Afonso F, Carmeliet G, Takeda H, Watt FM. 2008 The vitamin D receptor is a Wnt effector that controls hair follicle differentiation and specifies tumor type in adult epidermis. *PLoS ONE* **3**, e1483. (doi:10.1371/journal.pone.0001483)
  81. Demay MB. 2012 The hair cycle and vitamin D receptor. *Arch. Biochem. Biophys.* **523**, 19–21. (doi:10.1016/j.abb.2011.10.002)
  82. Morris RJ, Liu Y, Marles L, Yang Z, Trempus C, Li S, Lin JS, Sawicki JA, Cotsarelis G. 2004 Capturing and profiling adult hair follicle stem cells. *Nat. Biotechnol.* **22**, 411–417. (doi:10.1038/nbt950)
  83. Schmidt B, Horsley V. 2012 Unravelling hair follicle-adipocyte communication. *Exp. Dermatol.* **21**, 827–830. (doi:10.1111/exd.12001)
  84. Kiyozumi D, Osada A, Sugimoto N, Weber CN, Ono Y, Imai T, Okada A, Sekiguchi K. 2011 Identification of genes expressed during hair follicle induction. *J. Dermatol.* **38**, 674–679. (doi:10.1111/j.1346-8138.2010.01050.x)

85. Nissimov JN, Das Chaudhuri AB. 2014 Hair curvature: a natural dialectic and review. *Biol. Rev. Camb. Philos. Soc.* **89**, 723–766. (doi:10.1111/brv.12081)
86. Piérard-Franchimont C, Paquet P, Quatresooz P, Piérard GE. 2011 Mechanobiology and cell tensegrity: the root of ethnic hair curling? *J. Cosmet. Dermatol.* **10**, 163–167. (doi:10.1111/j.1473-2165.2011.00553.x)
87. Chacón-Martínez CA, Klose M, Niemann C, Glauche I, Wickström SA. 2017 Hair follicle stem cell cultures reveal self-organizing plasticity of stem cells and their progeny. *EMBO J.* **36**, 151–164. (doi:10.15252/embj.201694902)
88. Dawber R. 1996 Hair: its structure and response to cosmetic preparations. *Clin. Dermatol.* **14**, 105–112. (doi:10.1016/0738-081X(95)00117-X)
89. Franbourg A, Hallegot P, Baltenneck F, Toutaina C, Leroy F. 2003 Current research on ethnic hair. *J. Am. Acad. Dermatol.* **48**, S115–S119. (doi:10.1067/mjd.2003.277)
90. Erik B, Havitcioglu H, Aktan S, Karakus N. 2008 Biomechanical properties of human hair with different parameters. *Skin Res. Technol.* **14**, 147–151. (doi:10.1111/j.1600-0846.2007.00268.x)
91. Sayahi E, Harizi T, Msahli S, Sakli F. 2016 Physical and mechanical properties of Tunisian women hair. *Int. J. Cosmet. Sci.* **38**, 470–475. (doi:10.1111/ics.12313)
92. Aslan S, Evans TA, Wares J, Norwood K, Idelcaid Y, Velkov D. 2019 Physical characterization of the hair of Mexican women. *Int. J. Cosmet. Sci.* **41**, 36–45. (doi:10.1111/ics.12509)
93. Cloete E, Khumalo N, Ngoepe M. In press. Understanding curly hair mechanics: fibre strength. *J. Invest. Dermatol.* (doi:10.1016/j.jid.2019.06.141)
94. Macioce P. 2003 Viscoelastic damping 101. *Sound Vib.* **37**, 3.
95. Bhushan B. 2013 *Biophysics of human hair*. Berlin, Germany: Springer.
96. Khumalo NP, Stone J, Gumede F, McGrath E, Ngwanya MR, de Berker D. 2010 ‘Relaxers’ damage hair: evidence from amino acid analysis. *J. Am. Acad. Dermatol.* **62**, 402–408. (doi:10.1016/j.jaad.2009.04.061)
97. Wortmann FJ, Wortmann G, Popescu C. 2018 Kinetics of the changes imparted to the main structural components of human hair by thermal treatment. *Thermochim. Acta.* **661**, 78–83. (doi:10.1016/j.tca.2018.01.014)
98. Fernandes MM, Lima CF, Loureiro A, Gomes AC, Cavaco-Paulo A. 2012 Keratin-based peptide: biological evaluation and strengthening properties on relaxed hair. *Int. J. Cosmet. Sci.* **34**, 338–346. (doi:10.1111/j.1468-2494.2012.00727.x)
99. Khumalo NP, Gumede F. 2007 African hair length in a school population: a clue to disease pathogenesis? *J. Cosmet. Dermatol.* **6**, 144–151. (doi:10.1111/j.1473-2165.2007.00326.x)
100. Kuzuhara A. 2018 A Raman spectroscopic investigation of the mechanism of the reduction in hair with thioglycerol and the accompanying disulphide conformational changes. *Int. J. Cosmet. Sci.* **40**, 34–43. (doi:10.1111/ics.12429)
101. Boga C, Taddei P, Micheletti G, Ascari F, Ballarin B, Morigi M, Galli S. 2014 Formaldehyde replacement with glyoxylic acid in semipermanent hair straightening: a new and multidisciplinary investigation. *Int. J. Cosmet. Sci.* **36**, 459–470. (doi:10.1111/ics.12148)
102. Coderch L, Oliver MA, Carrer V, Manich AM, Martí M. In press. External lipid function in ethnic hairs. *J. Cosmet. Dermatol.* (doi:10.1111/jocd.12899)
103. Petzel-Witt S, Pogoda W, Wunder C, Paulke A, Schubert-Zsilavec M, Toennes SW. 2018 Influence of bleaching and coloring on ethyl glucuronide content in human hair. *Drug Test Anal.* **10**, 177–183. (doi:10.1002/dta.2206)
104. Kidwell DA, Lee EH, DeLauder SF. 2000 Evidence for bias in hair testing and procedures to correct bias. *Forensic Sci. Int.* **107**, 39–61. (doi:10.1016/S0379-0738(99)00148-6)
105. Oliver MA, Marti M, Coderch L, Carrer V, Kreuzer M, Barba C. 2019 Lipid losses and barrier function modifications of the brown-to-white hair transition. *Skin Res. Technol.* **25**, 517–525. (doi:10.1111/srt.12681)
106. Wortmann F, Schulze zur Wiesche E, Bourceau B. 2004 Analyzing the laser-light reflection from human hair fibers. II. Deriving a measure of hair luster. *J. Cosmet. Sci.* **55**, 81–93. (doi:10.1111/j.0142-5463.2004.00223\_6.x)
107. Sinclair D. 2007 Healthy hair: what is it? *J. Investig. Dermatol. Symp. Proc.* **12**, 2–5. (doi:10.1038/sj.jidsymp.5650046)
108. Velasco MV, Dias TC, Freitas AZ, Júnior ND, Pinto CA, Kaneko TM, Baby AR. 2009 Hair fiber characteristics and methods to evaluate hair physical and mechanical properties. *Braz. J. Pharm. Sci.* **45**, 153–161. (doi:10.1590/S1984-82502009000100019)



109. Baque CS, Zhou J, Gu W, Collaudin C, Kravtchenko S, Kempf JY, Saint-Léger D. 2012 Relationships between hair growth rate and morphological parameters of human straight hair: a same law above ethnical origins? *Int. J. Cosmet. Sci.* **34**, 111–116. (doi:10.1111/j.1468-2494.2011.00687.x)
110. Loussouarn G, El Rawadi C, Genain G. 2005 Diversity of hair growth profiles. *Int. J. Dermatol.* **44**, 6–9. (doi:10.1111/j.1365-4632.2005.02800.x)