



Review

Models for fingerprint pattern formation

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Abstract

There is currently no general agreement on the process by which fingerprint (epidermal ridge) patterns form. Nevertheless, many possible mechanisms have been proposed. Based on an extensive literature review and mathematical modeling we argue that the pattern arises as the result of a buckling (folding) process in a cell layer of the epidermis. Using this model we were able to explain the long-known observation that the pattern type is related to the geometry of the embryonal fingertip.

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1. Introduction

The growing importance of fingerprints (epidermal ridges) for our every-day life can hardly be overemphasized, especially in a time when biometric recognition techniques augment the

more traditional forensic applications. It is therefore not surprising that fingerprints have been an object of scientific curiosity for a long time. The focus of research included diverse fields such as anthropology, embryology, genetics, statistics of fingerprint patterns, biometric and forensic applications [1]. But despite the importance of fingerprint patterns and the significant empirical research a commonly accepted mechanism by which fingerprint patterns form has not yet emerged.

This lack of an agreement on the origin of fingerprints has clear implications for forensic science. Models for the distribution of minutiae and other important features for

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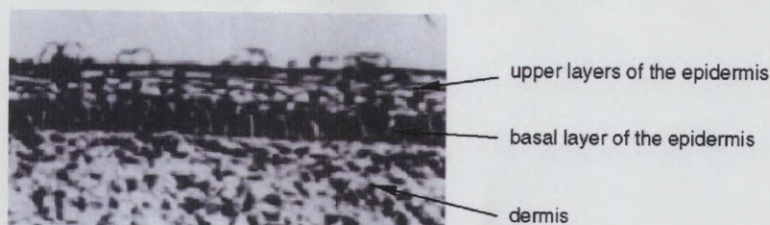


Fig. 1. Embryonal skin of the fingertip at the 10th week of pregnancy (from [8]).

identification mostly rely on statistical analysis because a mathematical model for the formation of these features is not available. Recently, the problem has been somewhat circumvented by efforts to produce realistic-looking fingerprints that can then be used for various purposes [2]. However, such simulations, no matter how realistic, provide no insight into the actual processes of fingerprint formation. Such insight could form a new approach for justifying the foundation of fingerprint evidence (especially concerning uniqueness), help to define measures of similarity, improve fingerprint recognition software and could be used to find quantitative measures of matching.

The path toward these goals is thorny. Biological phenomena such as the formation of fingerprints during embryogenesis are notoriously complicated and it is difficult to identify the crucial processes. Also, very often, important model parameters are unknown.

It is the purpose of this paper to review several mechanisms for fingerprint formation. Special focus is given to a model developed recently by the author and Newell [3–5]. Although this model uses advanced mathematical equations the basic ideas are quite simple and mathematical terminology will be avoided here. We will concentrate on the important concepts and not discuss all the subtle issues that came up during the modeling process [3,4].

The main topic of this paper is the physical mechanism for fingerprint formation. However, we also focus on the question how the direction of the ridges is determined and, connected to this topic, how the different pattern types (whorl, loop, arch) arise. In the first part of the paper we review the necessary biological material, some of which is not very well-known. In the second part we discuss the most important theories on fingerprint formation. Then we present our own ideas on the subject followed by a discussion and conclusions.

2. Biological background

The crucial events for human fingerprint formation start at the 10th week of pregnancy when the embryo has a size of just 80 mm. At that time embryonal skin already consists of two main parts: the epidermis sitting on top of the dermis. The epidermis is a typical epithelial tissue which is organized in several layers. The deepest layer on the interface to the dermis is called basal layer. The dermis of the 10th week has an amorphous appearance and consists of fibroblasts and collagen fibers (see Fig. 1) [6].

An important anatomical structure of the embryo's volar skin are the so-called volar pads. These are eminences of the volar surface at certain well-defined locations. They should not be confused with muscular eminences but rather consist of subcutaneous tissue and fat. In humans volar pads are found at the fingertips (apical pads), the distal part of the palm between the fingers (interdigital pads) and in the thenar and hypothenar areas (thenar and hypothenar pad), see Fig. 2.

In the human embryo, volar pads start to form at the 7th week of pregnancy. They continue to grow until about the 9th week and finally appear as high, rounded hillocks with a clearly defined base [7]. Later on they become smaller, appear less pronounced and their base merges with the surrounding tissue. Although apical and interdigital pads are still present in higher term embryos, and sometimes even at birth, the hand geometry eventually approaches the form of an adult. In human hands the hypothenar, the thenar and first interdigital pad are not well-developed and disappear early. On the foot the thenar pad merges with the first interdigital pad and forms what is called the hallucal pad, a large eminence below the base of the big toe. It is easily seen that areas that were covered by the embryonal volar pads are the sites where interesting patterns like whorls and loops appear, whereas, areas without pads usually exhibit

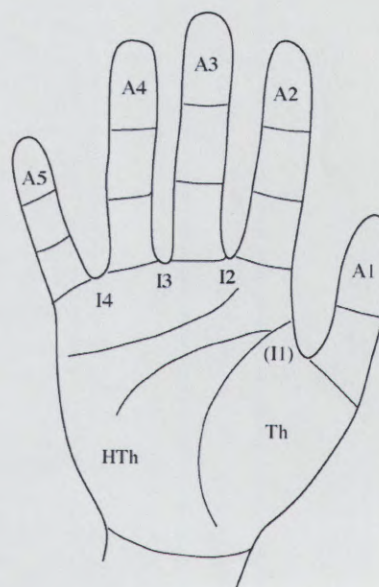


Fig. 2. The locations of the volar pads. A1–A5 denote the five apical pads on the fingertips. I1–I4 denote the interdigital pads. I1 is usually not well developed. Th denotes the thenar pad and HTh the hypothenar pad.

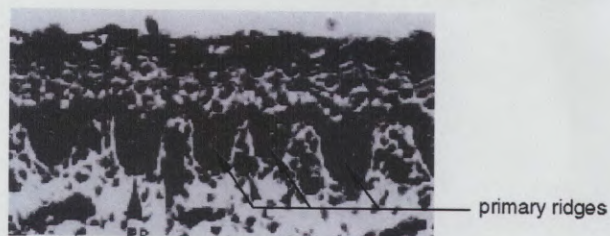


Fig. 3. The basal layer of the volar epidermis is folded in the 11th week of pregnancy. These folds are called primary ridges (from [8]).

parallel ridges only. This already indicates that the volar pads are important for the formation of fingerprint patterns.

Epidermal ridge development has been described by various researchers [8–17].

It is observed, starting from the 10th week, that the basal layer of the epidermis begins to appear slightly undulated. These undulations become quickly more pronounced and are called *primary ridges* (see Fig. 3). The pattern of the primary ridges already defines the future surface pattern. Therefore, if we want to understand how fingerprint patterns form we need to understand how the primary ridges arise.

Primary ridges do not form simultaneously on palms and soles. The timing of their formation was investigated by Bonnevie [9], Schaeuble [17] and Gould [10]. As a rule of thumb, the development on the foot is delayed by a week compared to the development on the hand. On the hand, primary ridges first form at the summits of the apical pads of the fingers and along the nail furrow (see Fig. 4(a)). Ridge formation is then initiated in the interdigital palm areas and in the midpalm along the flexion creases. Later on, thenar and hypothenar areas become ridged. Ridge development concludes with the proximal and then the middle phalanges of the

fingers. On the sole the sequence of ridge development is similar.

Bonnevie and Schaeuble studied the location on the volar pads where the ridges appear for the very first time. They called this place "*Papillaranlage*". There does not seem to be an English version of this concept, so we will use the name *ridge anlage* for it. According to Bonnevie and Schaeuble the ridge anlage is a small patch of volar skin characterized by intense cell proliferation at the time of ridge initiation and an overall increased thickness of the epidermis. In whorls the ridge anlage often coincides with the center of the whorl (see Fig. 4(b)); in a loop the ridge anlage coincides with the ridges making up the core of the loop, (see Fig. 4(c)).

The pattern on the fingertips is usually formed by three converging ridge systems (see Fig. 5(a)). The first one is the ridge system established by the ridge anlage (Bonnevie calls them pattern ridges), the second one is formed along the nail furrow (called mantel ridges), the third one forms just distally of the flexion crease (called basal ridges). When these ridge systems contact each other, both triradii and minutiae are formed. The triradii on the distal part of the palm arise in a similar fashion. Sometimes, the primary ridge pattern on the fingertip is established almost instantaneously as shown in Fig. 5(b). The ridges on the palm are formed parallel to the major flexion creases and ridge formation on the palm away from the volar pads starts along these creases [17]. Generally, there seems to be a lot of variation in the timing of ridge development. Gould found a 97 mm CRL (crown-rump-length) embryo with complete ridging of the distal phalanges, whereas, a 118-mm CRL embryo exhibited incomplete ridge development at the triradii in this area.

It is frequently mentioned [8,12] that during fetal development of the hand the number of ridges increases to keep up with



Fig. 4. (a) A schematic view on the locations of the first primary ridges. They start to form at the nail furrow and in a localized area in the middle of the pad (b) the center of a whorl forms, and (c) a loop forms (from [9]).



Fig. 5. (a) A whorl has formed, the three systems emanating from the ridge anlage, the nail furrow and the phalangeal crease start to merge and only the triradii are left unridged (b) A tented arch forms, ridges form almost instantaneously on the volar pad (from [9]).

the hand's growth [18]. This process of ridge multiplication is believed by many to be responsible for the formation of the many small defects (minutiae) in fingerprint patterns. There are strong clues that the ridge system significantly changes until its final appearance because the number of minutiae increases significantly in this time [18]. On the other hand, it does not seem likely that there is a dramatic increase in the number of ridges. From embryo pictures we have estimations of a ridge separation of about $35\ \mu\text{m}$ that are spread on a half cylinder with a radius of about $600\ \mu\text{m}$. On this half cylinder about 50 ridges could form, not much less than are usually found on a finger.

The period of primary ridge development ends at a fetal age of 19 weeks when the embryo has a size of 150 mm. Although the fingerprint pattern just begins to become visible on the skin surface at this time, the geometry of the ridge system is now established for life and will not change anymore. At the 14th week, sweat gland ducts start to project from the bottom of the primary ridges into the dermis. Together with the increased proliferation pressure of the cells in the primary ridges, they are believed to transfer the ridge pattern to the skin surface [13].

After primary ridge formation ceases at the 19th week, secondary ridges appear as folds between the primary ridges. Their shape is similar to the primary ridges but they are shallower and do not contain sweat glands. Secondary ridges can be found between all primary ridges by 24 weeks of pregnancy. Now dermal papillae, peg-like protrusions of the dermis, invade the epidermis in the space between primary and secondary ridges, thus forming double rows [19]. Although the appearance of the dermal papillae changes throughout life and sometimes obscures the secondary ridges, the geometry of the primary ridges remains the same.

As already hinted above, there is considerable evidence that the shape of the volar pads influences the ridge pattern. Most of the evidence comes from empirical studies, observations of dermatoglyphics of mammals and marsupials and studies of dermatoglyphics of malformed hands.

The first researchers that suggested a connection between volar pads and ridge configurations were Whipple [20] and Schlaginhaufen [21,22]. They studied the volar surface of primates and some other mammals. In many primate species, the volar pads do not regress and can still be observed in adults. The palms of such primates (see Fig. 6) show a close correlation between pads and ridge configurations that is hard to overlook. High, rounded pads display a whorl, with the center of the whorl sitting on the top of the pad. Here the ridges almost appear as elevation lines of the pads. Less prominent elliptic pads show elliptic configurations surrounding the line of highest elevation. Also loop and double-loop configurations may arise in this case.

When pads do not appear, likewise ridge configurations do not form and the epidermal ridges align in parallel fields. For instance, in humans the thenar pad and the first interdigital pad disappear early in the embryo and rarely give rise to configurations. Similarly, secondary pads give rise to configurations in places where they are not usually found, for instance, on the lower phalanges of the fingers of certain primates.



Fig. 6. The sole of *Papio hamadryas*. Summits are surrounded by concentric circles (whorls) and loop structures are found on the elongated elevations (from [22]).

It is important to point out that an eminence itself does not necessarily lead to configurations like whorls and loops. As an example we refer to the thenar area, which is already covered by a large eminence in the embryonic stage, whereas, the thenar pad disappears early. Another example is the calcar area (heel) of the foot which exhibits large eminences but which is not covered by volar pads. Pattern configurations are rarely found in these areas.

From the primate studies it was learned that high and rounded pads are related to the formation of whorl patterns. This hypothesis is supported by the work of Babler, who studied the formation of fingerprints in embryos [23–25]. Because, the volar pads become less prominent starting from the 10th week, we should expect to see more whorls if ridge formation is initiated early. Babler studied embryos which already exhibited recognizable patterns. He divided them in two groups, a group of embryos of 55–85 mm CRL and a group of embryos of 86–115 mm CRL. The first group can be thought of as embryos where ridge formation took place early and the second group as a control.

Babler observed that, in the early ridge differentiation group, 95.2% of all fingers displayed whorls, which is far more than the observed frequency in human populations, 4.8% displayed loops and no arches were found (compare finger and for all fingers together (from [26]) to the first row of Table 1). In the second group, the frequency of whorls was 30.4%, the frequency of loops was 52.2% and the frequency of arches 17.4%. These frequencies for whorls and loops are similar to the ones observed postnatally.

Further, there is strong evidence that asymmetries in the volar pad produce asymmetries in the ridge pattern. This

Table 1
Pattern type percentages of 24,518 Norwegians (from [26])

Finger	Whorls (%)	Radial loops (%)	Ulnar loops (%)	Arches (%)
All	25.65	5.81	61.14	7.40
I	35.04	0.34	60.71	3.91
II	28.89	23.98	30.66	16.47
III	16.22	2.31	70.44	11.03
IV	37.10	0.78	58.71	3.41
V	11.01	1.64	85.18	2.17

evidence was obtained by Bonnevie [26] who observed that the pattern frequency is not the same on all digits (see Table 1). For instance, digits I and IV often display whorls, and arches are more often found on digits II and III. Digit V has almost always ulnar loops, whereas, radial loops are almost exclusively found on digit II. Although different human ethnicities have different pattern frequencies and the frequencies differ between left and right hands, these observations are generally true.

Bonnevie [27] connected these observations to the geometry of the fingertip pad. She studied how symmetric or asymmetric the pads on the different digits are. Digit I and IV proved to be the most symmetric, and digit II and V proved to be the most asymmetric. Bonnevie explained these symmetry relations by the way the fingers form from the embryonic handplate. The thumb separates early from the other digits and preserves a fairly symmetrical appearance. Digits III and IV are still fairly symmetric because they are cut out from the middle of the handmass. The end fingers of the handmass (fingers II and V), however, display the greatest asymmetry because they are cut out at the end of the handmass (see Fig. 7). They are slanted toward the center of the handmass. Therefore, they have opposite asymmetry which is reflected by the high occurrence of radial loops on digit II and of ulnar loops on digit V.

3. Theories for ridge development

In this section, we discuss the existing theories that attempt to explain fingerprint formation. We refer to the theory that explains fingerprint formation by folding of the basal layer as the *folding hypothesis*. The idea that fingerprints are formed by a prepattern of either nerves or capillaries is called the *nerve hypothesis*. Finally we refer to the theory that claims that fingerprint patterns are first outlined in a prepattern of fibroblasts in the dermis as the *fibroblast hypothesis*.

3.1. The folding hypothesis and other mechanical hypotheses

The folding hypothesis was proposed for the first time in 1883 by Kollmann [28]. In the following, however, we focus on the more sophisticated work of Bonnevie on the subject.



Fig. 7. Cross-sections through the fingertips of the right hand of Bonnevie's embryo No. 83. The separation of fingers has just occurred and the pads have started to appear. Note that digit I (the thumb) appears fairly symmetric, digit II is slanted slightly to the ulnar direction, digits III and IV are slightly slanted radially and digit V is strongly slanted to the radial side (from [9]).

Bonnevie published a series of papers between 1924 and 1933 that contain an astonishing wealth of ideas. In a 1927 paper she described the processes leading to the primary ridges. She observed that the basal layer cells proliferate rapidly and appear cramped and compressed. To alleviate the compression cells in periodic distances move away toward the soft dermis that is easier penetrated than the stiffer upper epidermal layers. This way primary ridges arise.

The process that is described by Bonnevie is known in mechanics as a buckling process. The simplest example of such a process is a beam that is compressed. If the compression exceeds a certain threshold the beam inevitably bends away from the axis. The beam is then said to become unstable and undergo buckling. Buckling can also occur in two-dimensional structures. The model we are going to present later in this paper is a buckling model that is based on Bonnevie's observations.

The folding hypothesis, as it was described by Bonnevie, was accepted by German researchers of the 1930s such as Abel [29] and Steffens [30] and guided them in their thinking about fingerprint phenomena. However, this hypothesis did not gain universal acceptance.

Related to the folding hypothesis is the idea that mechanical forces determine the ridge patterns [31]. This idea was popularized by Harold Cummins, one of the most influential researchers in the field of dermatoglyphics. Based on his observations on malformed fingers he argued in a 1926 paper [32] that there is a connection between hand geometry and ridge patterns. He believed that this connection is established by growth forces acting on the fetal skin. But he did not specify how growth forces arise and how they form fingerprint patterns.

The folding hypothesis was rejected by some researchers by claiming that the primary ridges, in fact, arise as proliferations of the basal layer cells [20]. However, it is not at all obvious how cell proliferations can be organized in a way that they give rise to ridges. To our knowledge, no mechanism based on pure cell proliferations of the basal layer leading to fingerprint patterns has ever been suggested. On the other hand, increased cell proliferation of the lower layers of the epidermis is an important ingredient of Bonnevie's ideas. Further, it is plausible that the topology of the primary ridge pattern arises by folding, and then, once the ridges have been created, their depth is increased due to cell proliferations.

To make the folding theory more credible (or any other theory that is based on growth stresses and volar pad geometry) it is necessary to test it. This should be done by identifying sources for the growth stresses that are supported by biological observations and by studying the implied stress distribution and corresponding patterns.

3.2. The nerve hypothesis

There is a lot of evidence that there are connections between the system of nerves and blood vessels and the positioning of the primary ridges.

For example, Hirsch [13] and Schweichel found nerve fibers surrounded by blood vessels (thus forming what they call a *vessel-nerve pair*) in the dermis projecting to the base of the

primary ridges. But it is not clear whether the vessel–nerve pairs determine the formation of the primary ridges or if, vice versa, the vessel–nerve pairs are attracted to the site of the primary ridges once these have formed. The authors speculate that the absence of epidermal ridges and unusual dermatoglyphic patterns could be caused by neurohypotrophies. This was confirmed by Schaumann [33] who observed unusual dermatoglyphic patterns in cases of spina bifida. The severity of the syndrome was correlated with the abnormality of the dermatoglyphic patterns, in some cases no epidermal ridges could be found on the skin surface at all.

These ideas are related to the ones by Blechschmidt [34] who claimed that the ridges simply follow the network of capillaries underneath them. Unfortunately, he limited his observations to the distal and proximal parts of the fingertip in order to avoid the “complicated individual development” in the center of the fingertip. The center of the fingertip is really the location of the interesting patterns. Unless there is data confirming a relationship between ridges and capillaries in this area as well, Blechschmidt’s observations can be dismissed as mere coincidence.

More elaborately formulated, and with more evidence, the nerve theory was presented in a 1986 work of Dell and Munger [35]. Using light and electron microscopy of rhesus monkey fetuses, these authors identified growth cones of nerve fibers that project to the epidermis. These growth cones are organized hexagonally with a distance of 40 μm between each other. This approximately coincides with the separation of the primary ridges. This innervation takes place in embryos of 55 mm CRL well before any primary ridges become visible. The authors speculated that the afferent nerve fibers provide a grid that could modulate the spacing and the arrangement of the ridges. Abnormal fingerprints could reflect abnormalities in the nervous system. Further, Dell and Munger pointed out that other epidermal organs are also proposed to be neurally induced. Examples are teeth, taste buds and feathers. These findings on monkey embryos have been confirmed in a follow-up study by Moore and Munger [36] on human embryos.

All these studies suggest that the nervous system plays an important role in the development of the ridge system. However, it seems unlikely that the nerves generate the pattern all by themselves. For instance, the ridge direction cannot be determined by the hexagonal pattern of the innervating axons. Furthermore, it is not obvious how the larger scale configurations like whorls and loops are formed and what role the pad geometry would play in this process.

Further insight into the relationship between the nervous system and the ridge pattern comes from two papers by Morohunfolo et al. [37,38]. The authors studied the development of the primary ridges in the opossum *Monodelphis domestica* in which the nerve fibers to the left hindpaw were removed. It was observed that primary ridges still formed in the affected leg with no change in ridge separation but ridge initiation was delayed and ridge depth decreased. This again suggests that the nervous system is involved in ridge formation but that it is not the primary pattern forming system.

Another interesting link between the nerve system and fingerprint patterns was observed by Bonnevie. She found that the embryonic fingertip is innervated by two main nerves. Both of them project toward the skin surface and converge to each other (see Fig. 10). Bonnevie noticed that they finally end underneath the proximal border of the ridge anlage. She speculated that the nerves could define the location of the ridge anlage although she admitted that causality is difficult to prove in that case. Her observation holds also true in cases where *two* ridge anlagen are observed. In these cases, the nerve twigs fail to converge and a nerve projects to each ridge anlage (see Fig. 11). Bonnevie believed that this phenomenon is the reason for so-called accidental patterns, such as double loops or more complex whorls. This relationship between ridge anlage and nerve innervation was recently confirmed by Dell and Munger [35] and Moore and Munger [36].

3.3. The fibroblast hypothesis

It is well-known from mathematical topology that structures like loops and triradii are generic features of ridge systems [39]. Nevertheless, some pattern forming systems have been related to fingerprints solely based on the fact that they exhibit features such as triradii and loops.

An example is a 1978 paper by Green and Thomas [40] that deals with patterns arising in cultures of disaggregated human epidermal cells. The authors observed that keratinocytes in petri dishes form, after 30–40 days, directional patterns that are reminiscent of whorls or triradii. Another example is patterns that were obtained by Elsdale and Wasoff [41] in fibroblast cultures. Fibroblasts are undifferentiated elongated cells in the dermis that can potentially differentiate into muscle, connective tissue or fat cells. In culture, fibroblasts tend to align themselves and form patterns with a ridge structure. But apart from similarities in the topology there does not seem to be a lot of evidence that these patterns have something to do with fingerprint patterns. The flow of the pattern looks quite different than the one of fingerprints and no ridge separation length is defined.

The fibroblast hypothesis has received considerable interest from the mathematical side and Benthil developed a model [42,43] on its basis that was supposed to model fingerprint formation. This model is the two-dimensional version of a model first developed by Murray and Oster [44,45] to describe the interaction between fibroblasts and extracellular matrix and the pattern-forming ability of these processes. A system of differential equations is set up based on the observation that fibroblasts can generate strong tensile forces that act on the surrounding extracellular matrix [46]. It also takes into account that fibroblast cells have been observed to move toward areas of greater stickiness, a phenomenon called *haptotaxis*. Unfortunately, besides the topological resemblance the model uses few biological observations and does not explain a lot. Further, the numerical simulations of the equations are not convincing.

Another theory developed by Fleury links epidermal ridge alignment to both fibroblast structures and some sort of buckling process [47]. The problem of this theory is, again, the

lack of evidence for a connection between fibroblast patterns and fingerprint patterns.

4. A model based on a buckling process

4.1. Idea of the model

After reviewing the extensive literature dealing with fingerprint formation we think that the folding hypothesis is the most promising for understanding fingerprint formation. Following Bonnevie's ideas we hypothesize that *the epidermal ridge pattern is established as the result of a buckling process acting on the basal layer of the epidermis.*

The cytoskeleton of the basal layer cells are connected with each other by desmosomes. The basal layer gains further structural support by hemidesmosomes that attach to the basal lamina, a thin protein sheet that acts as a seal between dermis and epidermis. Therefore, the basal layer is an elastic sheet that can withstand forces and resist bending. Bonnevie, Schaeuble and others observed intense cell proliferation in the basal layer just prior to primary ridge development. Although the surrounding structures also grow it is plausible that the basal layer cells grow fastest. As the basal layer cells are confined to their space and cannot expand compressive stress builds up in the basal layer. If the stress in the basal layer exceeds a certain limit buckling occurs. The folds grow toward the dermis, which is known to be softer than the upper layers of the epidermis.

An important argument for the folding hypothesis is based on the fact that it is directly connected to concepts like forces and curvature. Therefore the folding hypothesis allows us to tackle the question why fingerprint patterns are related to the pad geometry. Later in this paper we will illustrate how, based on the folding hypothesis, this connection can be explained.

Modeling this situation is tricky because the involved processes are complicated and the mechanical properties of the involved tissues not very well known. Therefore, we consider a simplified situation that contains the essence of the process (see Fig. 8). We assume that the basal layer is a thin, curved elastic sheet that is put under compressive stress. The sheet is generally not compressed at the same degree in all directions. Movement of this sheet is resisted upwards (toward the upper layers) and, to a lesser degree, downwards (toward the dermis). In the model, treating the surrounding layers as springs incorporates this situation.

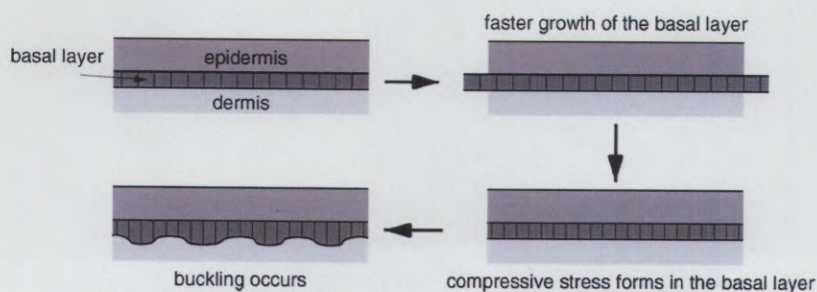


Fig. 8. A schematic view on the buckling model. Differential growth produces compressive stress in the basal layer. The surrounding tissue resists in a spring-like manner out-of-plane displacement of the basal layer.

This situation can be easily translated into mathematics resulting in two coupled partial differential equations that are not simple at all but can be approached using standard analyses. These equations are the von Karman equations of elasticity, originally developed for engineering applications (see [48]).

The von Karman equations allow the determination of the pattern type and the ridge spacing. They also tell us, depending on the equation parameters, the ridge direction. We found out that in most cases *ridges are the preferred pattern and that these ridges are formed perpendicular to the largest stress.* Interestingly it turned out that another pattern type is also possible in certain circumstances—a dot pattern arranged in a hexagonal fashion. Interestingly, such dot patterns do in fact appear on the palms of certain marsupials such as the koala (see [5] for more details).

These analyses shed light on the pattern forming process at the time when primary ridges are first initiated. They tell us about the pattern type, ridge direction and ridge spacing. But they do not tell us how the ridge system develops in the subsequent time until its final appearance. This is due to two reasons. At first, the von Karman equations are not valid anymore once the ridges reach a certain depth. Secondly, it is very likely that buckling does not completely shape the ridge system alone and other biological mechanisms are also involved.

4.2. The generation of stress

As the next step we have to understand how the stress distribution in the basal layer is generated. There are two important mechanisms:

4.2.1. Boundary effects

These effects are important for understanding why the ridge direction in certain areas is almost always the same in different humans. To understand the basic idea refer to Fig. 9. Here the major palm flexion creases, the wrist crease, the phalangeal creases and the nail furrow are shown as thick lines. We notice that the ridges run parallel to these lines. In other words, *the ridges tend to align themselves parallel to the creases and furrows.* Of course, this is only true for the creases that arise prior to ridge formation and not for the ones that form later. At this point, we do not have embryological evidence that the wrist crease is formed before ridges do. This, however, is clearly true

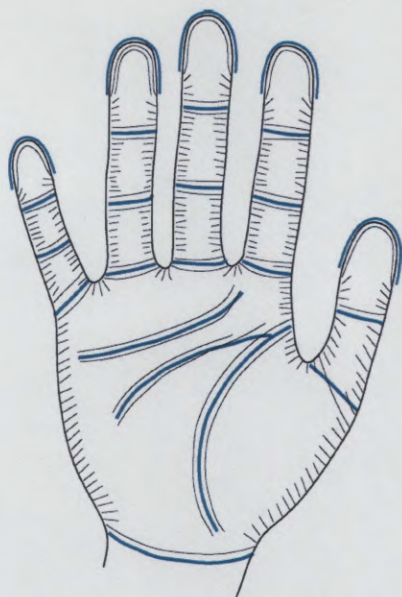


Fig. 9. The relation between folds and furrows (thick lines), the periphery of the palm and the epidermal ridges are shown. The ridges tend to run parallel to the thick lines and perpendicular to the margin of the palm.

for the other creases mentioned and the nail furrow. Further, we notice that there is a relation between ridge direction and the margin of the palm. We see that *the ridges usually arrive at a steep angle at the periphery of the volar surface*. This angle is often very close to a right angle and almost never less than 45° . Exceptions to these observations are infrequent and usually occur if the ridges are subject to conflicting requirements and some kind of compromise has to be found.

The conclusions from the models provide us with a framework to understand these observations. Remember, that we consider an expanding cell sheet in which compressive stress is generated due to *resistance* of the surrounding structures. It is likely that the nail furrow and the flexion creases resist expansion. In contrast it is plausible that the margin of the palm provides much less resistance to expansion. As the basal layer cannot expand toward the creases it is subjected to compressive forces acting perpendicular to the creases. Since the ridges align themselves along the lines of smallest stress, they form along the creases, as it is actually observed. The situation is exactly opposite at the margin of the palm. Because, basal layer expansion is not resisted here, there are no forces perpendicular to the margin of the palm. This is clearly the direction of smallest stress. Hence, the ridges align perpendicular to the palm periphery.

4.2.2. Shrinkage of the volar pads

If a curved surface is deformed stress may arise due to curvature. For example, assume you have a hollow ball filled with air. If the air is evacuated the underpressure makes the ball shrink slightly. At the same time compressive stress increases in the ball until the induced stress balances the underpressure. This stabilizing effect is often used in architecture for the design of bridges and domes [48]. The induced stress is

proportional to the curvature of the surface and the amount of shrinkage.

A similar effect is important for fingerprint development. At the time of primary ridge formation the volar pads become less dominant and shrink (compared to the other structures). Therefore, compressive stress is induced that augments the stress from the boundary effects. Because, the process depends on the individual curvature of the pad it is responsible for much of the individuality of a fingerprint.

Looking at several of Bonnevie's pictures of cross-sections through fetal fingertip pads (like in Fig. 11) we notice that the usually nicely rounded outline of the pad often becomes flat or even slightly concave at the ridge anlage. Strangely, almost nobody has given this phenomenon much attention. Bonnevie attributed it to the fact that buckling has taken place and the stress is relieved. However, this argument does not explain the degree of concavity found in some specimens. Bonnevie's observations have been confirmed by Schaeuble [17] at the ridge anlagen of the interdigital pads and more recently by Moore and Munger [36].

This change in concavity at the ridge anlage indicates that the shrinkage is especially large in that area. Indeed, it seems as if the epidermis is pulled in by some force here. We may even speculate about the probable origin of this force. The main clue is provided by Figs. 10 and 11 which show the papillary nerve projecting to the ridge anlage. It is plausible that the presence of the nerve induces forces that pull in the epidermis. For instance, the nerve could absorb fluids and create an underpressure in the volar pad below the ridge anlage. In fact, this fluid absorption could possibly be the very mechanism for pad shrinkage. If this interpretation is true, it would mean that the position of the ridge anlage is indeed caused by the incoming papillary nerves and confirm the importance of the nervous system on the development of epidermal ridges. Because the largest shrinkage occurs in the area of the ridge anlage (usually close to the summit of the volar pad), the stress is largest in that area and it is not surprising that ridge formation takes place there first.

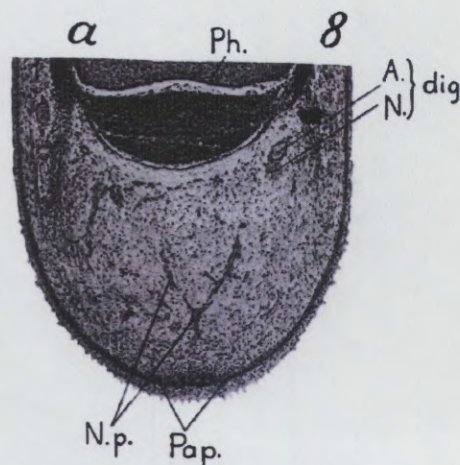


Fig. 10. A cross-section through an embryonic fingertip. The two papillary nerves (N.p.) converge towards the ridge anlage (Pap.) (from [9]).

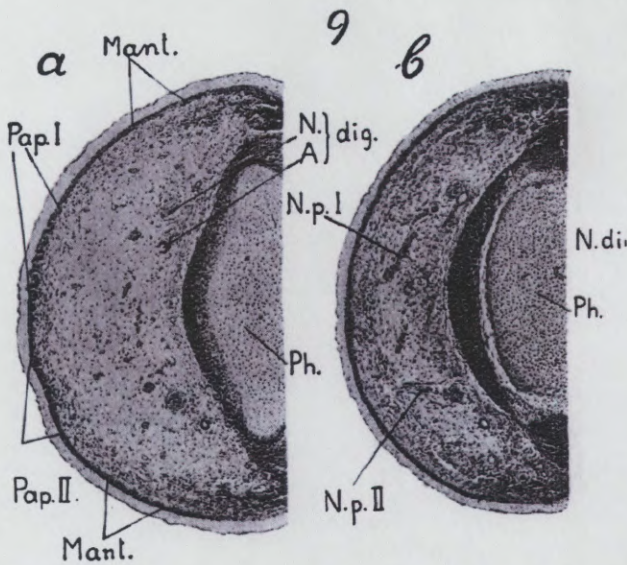


Fig. 11. Two cross-sections through an embryonic fingertip. The left figure reveals that two ridge anlagen are present. A more proximal cut shows incomplete convergence of the papillary nerves (N.p. I and N.p. II) that point to the centers of the ridge anlagen {Pap. I and Pap. II} (from [9]).

4.3. The connection between pad geometry and pattern type

Now we will explain how the combination of boundary effects and pad shrinking leads to the most common fingerprint configurations and what role the volar pad geometry plays in this process. Let us consider the situation at the fingertips. To introduce some useful definitions refer to the illustration of a finger given in Fig. 12. Here the position of the ridge anlage and directions A–F that radiate from it are given.

The situation is rather straight-forward near the flexion crease and the nail furrow. In these areas boundary effects dominate. Therefore, the largest stress is perpendicular to these features and the ridges are aligned parallel to the flexion crease

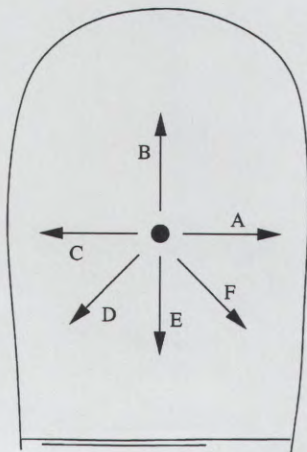


Fig. 12. The fingertip, the location of the ridge anlage and certain directions radiating from it.

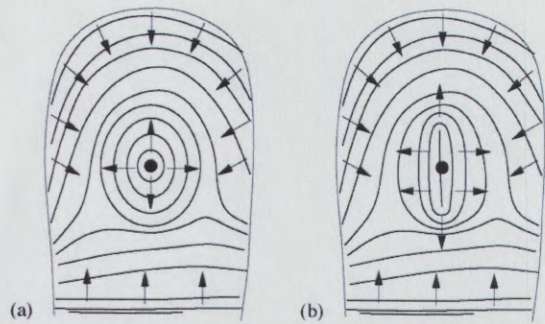


Fig. 13. The forces shaping a whorl: (a) the volar pad is high, rounded and pad shrinking in the area produces radial stress away from the ridge anlage and (b) the volar pad is less pronounced and stress along A–C dominates in the center.

and the nail furrow. But what about the center of the fingertip where all the interesting patterns are?

At first, consider that we have a highly rounded, almost spherical, pad with the ridge anlage close to the summit. At the ridge anlage, curvature is present in all directions. Shrinking induces large stress radiating from the ridge anlage. Because, the ridges form perpendicular to the largest stress a whorl forms. This situation is illustrated in Fig. 13(a).

Let us now imagine that the pad is somewhat less pronounced. In this case, the curvatures along A–C exceed the ones along B–E, because the finger is significantly curved along A–C even in the absence of apical pads. Therefore, the stress along A–C is larger than the one along B–E. The stress along A–C dominates at the ridge anlage and the center of the whorl becomes elongated. See Fig. 13(b) for an illustration.

As the pad becomes flatter the stress induced by shrinking decreases because the amount of curvature decreases and not much further shrinkage takes place that could result in stress. Therefore, the radial stress along directions D and F decreases. At some point the radial stress along these directions is overpowered by the boundary stress. The largest stress is now across to D and F, which makes the ridges align parallel to D and F. A tented arch has formed. See Fig. 14(a) for a visualization. If the shrinkage of the pad is decreased further, hardly any stress is generated away from the boundaries. The

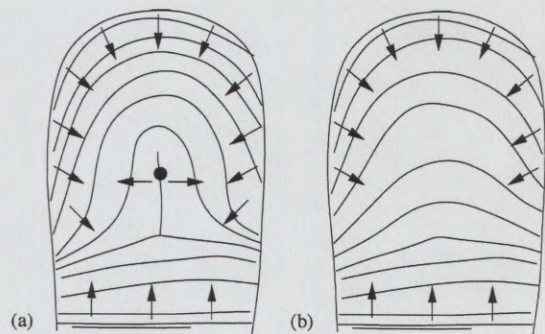


Fig. 14. The forces shaping tented arches and arches. (a) For a flatter pad little stress is generated in direction D–F. Boundary effects dominate and a tented arch arises, (b) If the pad is even flatter and little normal pressure is applied the boundary forces dominate the stress pattern and arches form.

stress field is then dominated by the boundary stress, resulting in an arch. This situation is seen in Fig. 14(b).

To understand how loops emerge consider a tented arch and assume that the pad is asymmetric. Let us assume that the pad is slanted to the radial side, the case for the ulnar side is equivalent. The location of greatest curvature for each cross-section can now be found on a curve radial to the ridge anlage, as demonstrated in Fig. 15(a). The stress produced by the shrinkage of the pad at the ridge anlage is predominantly along A–C and the ridges form along B–E. An ulnar loop forms in this situation if the boundary forces from the ulnar side have a larger effect on the stress field at the center of the pad than the boundary forces from the radial side. In this case, the ridges in the center are slightly bent toward the ulnar side. Even a small change of this kind destroys the tented arch (a rare configuration after all) and creates a loop (the most common configuration). But why is the effect from the ulnar side larger than the one from the radial side? The asymmetry of the pad implies more curvature on the radial side than on the ulnar side. Therefore, it is harder for the boundary forces from the radial side to have an effect in the center of the fingertip because they have to get 'around' the large curvature of the radial side. The effect from the ulnar side dominates, bends the ridges toward the ulnar side and creates an ulnar loop.

These heuristic arguments were confirmed by finite element computer simulations (see [5]). These simulations determine the stress in the fingertip for a given fingertip shape. However, there is another important consistency: the simulations further tell us that the stress is largest in the center of whorls and loops and along the nail furrow – where the ridges, in fact, appear first – and is smallest in the area of triradii—where ridge formation takes place last.

Having the stress field we can now calculate the buckling pattern. We use the stress field as input to the von Karman equations. The equations are solved using a spectral method.

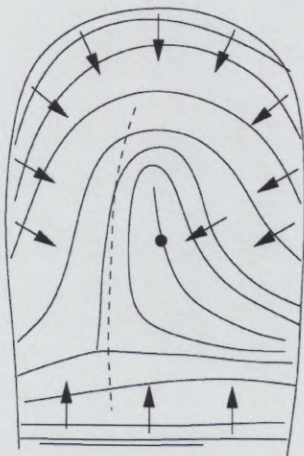


Fig. 15. The forces shaping loops. If we have an asymmetric pad (the line of the location of greatest radius is indicated by the dashed line) the pattern becomes asymmetric as well. For moderate pad elevation stresses in direction A–C dominate. The direction of the ridges in the center of the pad is influenced by the boundary forces.

This way we obtain a buckling pattern that, in many respects, resembles actual fingerprint patterns (see Fig. 15 and [4,5]).

5. Discussion

The presented theory provides a consistent framework for many aspects of fingerprint pattern formation. It gives an explanation for the empirically found connection between fingertip geometry and pattern type. It predicts the correct timing of pattern spread. The three most common fingerprint types can be reproduced.

The patterns obtained in our simulations (see Fig. 16 for an example) reproduce the general "flow" of fingerprint patterns nicely. Also, the "texture" of the minutiae is close to the one we observe in real fingerprints. It sometimes happens that the ridges change their direction sharply as they transition from one patch to another. Such a situation can be seen in Fig. 16 above the triradii. Although such situations occur in real fingerprints they are quite rare.

The branches and endings in our simulations mostly occur in two circumstances. They show up when the ridges diverge from each other and new ridges are inserted. Further, they arise in regions where almost parallel ridge patches meet each other (such as the triradii) and the cores of whorls and loops. Our observation is consistent with statistics on fingerprint data in forensics [49] showing that minutiae in such areas are more frequent than at the periphery. In our simulations we obtained very few minutiae at the periphery, where they are in fact not that rarely observed in real fingerprints. Minutiae at the periphery could arise due to growth of the finger that makes insertion of new ridges necessary. At this point we have not attempted to model such effects.

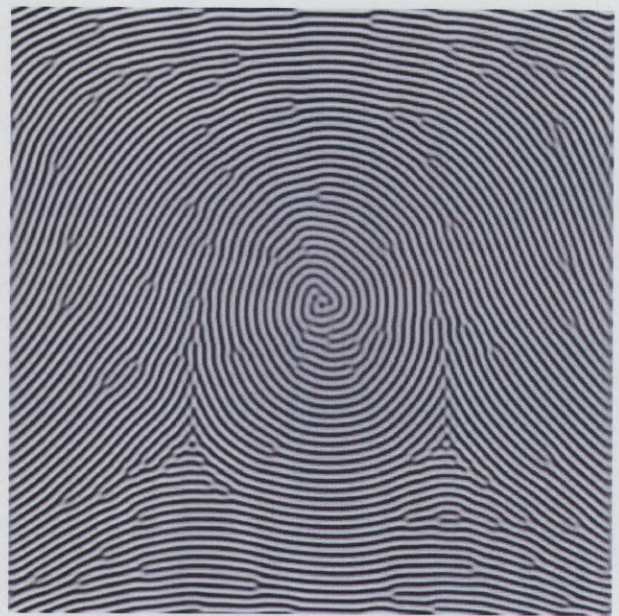


Fig. 16. A whorl pattern obtained using approach 1. Ridge formation takes place simultaneously over the surface. The characteristic features of the whorl including the dislocations are well-captured. However, note the sharp change in ridge direction above the triradii.

Changing the initial conditions or parameters slightly results in a distinct change in the placement of the minutiae. In this sense, the minutiae are quite sensitive to their “environment”. This is the origin for the well-observed fact that fingerprints are indeed unique and can be used for identification purposes.

We believe that unbiological features in our simulations do not negate the validity of our approach. Quite the contrary, the von Karman equations were enormously helpful to understand the onset of pattern formation. The results we obtained from the analysis of the equations are consistent with the biological observations and helped us to gain a better understanding how the pattern is laid out. However, in our investigations we limited ourselves to observations that are determined at the beginning of the buckling process like ridge spacing, pattern type and ridge direction. Therefore the model cannot be expected to give a quantitatively correct description for the minutiae because these features form in the weeks after the folding process has been initiated. Unfortunately, embryological observations concerning the development of minutiae are very scarce. Once such observations become available our model can serve as a basis for a new quantitative theory of minutiae.

6. Conclusion

We finally formulate our complete hypothesis on the development of epidermal ridges as follows:

The epidermal ridge pattern is established as the result of a buckling instability acting on the basal layer of the epidermis and resulting in the primary ridges.

The buckling process underlying fingerprint development is controlled by the compressive stress formed in the basal layer.

The compressive stress that determines ridge direction is itself determined by boundary forces acting at creases and the nail furrow and shrinkage of the volar pads, which is most pronounced close to the ridge anlage.

Referring to this hypothesis we can suggest the following scenario of ridge development

- The fingers separate from each other at the 6th week of pregnancy. This process leads to asymmetries in finger shape, especially in finger II and V.
- Volar pads appear on the fingertips and in certain areas of the palm at around the 7th week. In the following weeks the volar pads become more pronounced and slowly subside starting from the 10th week.
- At about the 11th week differential growth is observed in the basal layer in the epidermis.
- This growth is resisted by creases and folds in the tangential direction and causes compressive stress.
- Further compressive stress arises due to the shrinkage of the pads. This effect is most pronounced in the area above the nerve twigs innervating the volar pad, possibly due to absorption of fluids.

- The stress in the basal layer leads to buckling, the ridges form perpendicular to the greatest stress.
- Depending on the height and asymmetry of the pad, and the magnitude of pad shrinking, whorls, loops, arches or accidental patterns form.
- Ridges start to form at the nail furrow, the creases and the ridge anlage and spread over the fingertips and the remaining volar surface in the course of several weeks.
- This process, although initiated by buckling, is likely modulated by biological effects such as changes in cell properties in different locations of the primary ridges and nonlinear material properties.
- In the course of ridge maturation, the number of minutiae increases, possibly due to growth of the fingertip.

One way to estimate the quality of our work is to compare the real and simulated patterns. They surely have a lot in common, such as the topology, an established ridge separation length and similar ridge direction. Differences should be the cause of further work such as the behavior in regions of rapid ridge direction change or the stiffness of the simulated pattern in some regions.

Even more important than the resemblance of reality and simulation is the fact that the ideas in this work integrate the mainstream ideas on fingerprints. Our model confirms that:

- Primary ridges are formed as the result of a buckling process.
- Ridges form perpendicular to the lines of greatest stress.
- Volar pad geometry influences the fingerprint pattern.
- The nervous system influences ridge formation.
- Although ridges are the usual pattern, dot patterns are possible under certain circumstances.
- After the buckling instability has taken place and the ridge pattern is established, cell proliferations may increase the depth of the primary ridges.
- Minutiae, sensitive to initial conditions, are formed.

Further the model does not contradict biological effects that are reported in the literature and may influence the postbuckling behavior.

The mathematical techniques provide the means of tying these ideas together. For example, the analysis of the von Karman equations provide the link between ridge direction and the stress. Computer experiments provide the possibility to test how certain forces on the basal layer result in a stress pattern that in turn establishes the buckling pattern. Based on this work, we were able, for the first time, to suggest specific growth forces that make the connection between pad geometry and pattern type and are biologically motivated.

This work also clarifies the extent to which genetics influences fingerprint patterns. As we have argued, general ridge direction and the pattern type depend on the geometry of the volar pads and the timing of their shrinking process. These factors are very likely genetically controlled. On the other hand, the distribution of the minutiae is sensitive to the exact embryonal environment and therefore highly random and unique.

References

- [1] H. Cummins, C. Midlo, *Finger Prints Palms and Soles*, Research Publishing Company Inc., 1976.
- [2] R. Cappelli, Synthetic fingerprint generation, in: D. Maltoni, D. Maio, A.K. Jain, S. Prabhakar (Eds.), *Handbook of Fingerprint Recognition*, Springer, 2003.
- [3] M. Kücken. On the formation of fingerprints. PhD thesis, University of Arizona, 2004.
- [4] M. Kücken, A.C. Newell, A model for fingerprint formation, *Europhys. Lett.* 68 (2004) 141–146.
- [5] M. Kücken, A.C. Newell, A model for fingerprint formation, *J. Theor. Biol.* 235 (2005) 71–83.
- [6] K.A. Holbrook, Structure and function of the developing human skin, in: L.A. Goldsmith (Ed.), *Biochemistry and Physiology of the Skin*, Oxford University Press, 1983.
- [7] H. Cummins, The topographic history of the volar pads (walking pads; Tastballen) in the human embryo. *Contributions to Embryology* No. 113, 20 (1929) 105–126.
- [8] W.J. Babler, Embryologic development of epidermal ridges and their configurations, in: C.C. Plato, R.M. Garruto, B.A. Schaumann (Eds.), *Dermatoglyphics: Science in Transition*, Wiley-Liss Inc., 1991.
- [9] K. Bonnevie, Die ersten Entwicklungsstadien der Papillarmuster der menschlichen Fingerballen, *Nyt Magazin for Naturvidenskaberne* 65 (1927) 19–56.
- [10] E.S. Gould. A topographic study of the differentiation of the dermatoglyphics in the human embryo, PhD thesis, Tulane University, 1948.
- [11] I.S. Guseva, W.M. Stambrovskaya, S.D. Bezsubik, On the problem of the formation of papillary patterns on human fingers (in Russian), *Arch. Anat. Histol. Embryol.* 80 (1981) 75–80.
- [12] A.R. Hale, Morphogenesis of volar skin in the human fetus, *Am. J. Anat.* 91 (1951) 147–180.
- [13] W. Hirsch, Morphological evidence concerning the problem of skin ridge formation, *J. Ment. Defic. Res.* 17 (1973) 58–72.
- [14] M. Okajima, Development of dermal ridges in the fetus, *J. Med. Genet.* 12 (1975) 243–250.
- [15] M. Okajima, L. Newell-Morris, Development of dermal ridges in the volar skin of fetal pigtailed macaques (*Macaca nemestrina*), *Am. J. Anat.* 183 (1988) 323–337.
- [16] L.S. Penrose, P.T. O'Hara, The development of epidermal ridges, *J. Med. Genet.* 10 (1973) 201–208.
- [17] J. Schaeuble, Die Entstehung der palmaren Triradien, *Z. Morphol. Anthropol.* 31 (1932) 403–438.
- [18] A.R. Hale, Breadth of epidermal ridges in the human fetus and its relation to the growth of the hand and foot, *Anat. Rec.* 105 (1949) 763–776.
- [19] M. Okajima, Dermal and epidermal structures of the volar skin, in: W. Wertelecki, C.C. Plato, D. Bergsma (Eds.), *Dermatoglyphics—Fifty Years Later*, Alan R. Liss Inc., 1979.
- [20] I. Whipple, The ventral surface of the mammalian chirodium with especial reference to the condition found in man, *Z. Morphol. Anthropol.* 7 (1904) 261–368.
- [21] O. Schlaginhaufen, Das Hautleistensystem der Primatenplanta unter Mitberücksichtigung der Palma Teil I, *Morphol. Jahrbuch* 33 (1905) 577–671.
- [22] O. Schlaginhaufen, Das Hautleistensystem der Primatenplanta unter Mitberücksichtigung der Palma Teil II, *Morphol. Jahrbuch* 34 (1906) 1–125.
- [23] W.J. Babler. The prenatal origins of populational differences in human dermatoglyphics. PhD thesis, University of Michigan, 1977.
- [24] W.J. Babler, Prenatal selection and dermatoglyphic patterns, *Am. J. Phys. Anthropol.* 48 (1978) 21–28.
- [25] W.J. Babler, Epidermal ridge differences, in: W. Wertelecki, C.C. Plato, D. Bergsma (Eds.), *Dermatoglyphics—Fifty Years Later*, Alan R. Liss Inc., 1979.
- [26] K. Bonnevie, Studies on papillary patterns in human fingers, *J. Genet.* 15 (1924) 1–111.
- [27] K. Bonnevie, Was lehrt die Embryologie der Papillarmuster über ihre Bedeutung als Rassen- und Familiencharakter Part I and II, *Z. Indukt. Abstamm. Ver.* 50 (1929) 219–274.
- [28] A. Kollmann, *Der Tastapparat der menschlichen Rassen und der Affen in seiner Entwicklung und Gliederung*, Voss Verlag, 1883.
- [29] W. Abel, Kritische Studien über die Entwicklung der Papillarmuster auf den Fingerbeeren, *Z. Menschliche. Vererb. Kons.* 21 (1938) 497–529.
- [30] C. Steffens, Über Zehenleisten bei Zwillingen, *Z. Morphol. Anthropol.* 37 (1938) 218–258.
- [31] J.J. Mulvihill, D.W. Smith, The genesis of dermatoglyphics, *J. Pediatr.* 75 (1969) 579–589.
- [32] H. Cummins, Epidermal-ridge configurations in developmental defects, with particular reference to the ontogenetic factors which condition ridge direction, *Am. J. Anat.* 38 (1926) 89–151.
- [33] B. Schaumann, Clinical aspects of dermatoglyphics, in: C.C. Plato, R.M. Garruto, B.A. Schaumann (Eds.), *Dermatoglyphics: Science in Transition*, Wiley-Liss Inc., 1991.
- [34] E. Blechschmidt, Die embryonalen Gestaltungsfunktionen der menschlichen Oberhaut, *Z. Morphol. Anthropol.* 54 (1963) 163–172.
- [35] D.A. Dell, B.L. Munger, The early embryogenesis of papillary (sweat duct) ridges in primate glabrous skin. The dermatotopic map of cutaneous mechanoreceptors dermatoglyphics, *Comp. Neurol. J.* 244 (1986) 511–532.
- [36] S.J. Moore, B.L. Munger, The early ontogeny of the afferent nerves and papillary ridges in human digital glabrous skin, *Dev. Brain Res.* 48 (1989) 119–141.
- [37] K.A. Morohunfolo, T.E. Jones, B.L. Munger, The differentiation of the skin and its appendages. I. Normal development of the papillary ridges, *Anat. Rec.* 232 (1992) 587–598.
- [38] K.A. Morohunfolo, T.E. Jones, B.L. Munger, The differentiation of the skin and its appendages. II. Altered development of papillary ridges following neuralectomy, *Anat. Rec.* 232 (1992) 599–611.
- [39] T. Passot, A.C. Newell, Towards a universal theory for natural patterns, *Phys. D* 74 (1994) 301–352.
- [40] H. Green, J. Thomas, Pattern formation by cultured human epidermal cells: development of curved ridges resembling dermatoglyphs, *Nature* 200 (1978) 1385–1388.
- [41] T. Elsdale, F. Wasoff, Fibroblast cultures and dermatoglyphics: the topology of two planar patterns, *Roux Arch. Dev. Biol.* 180 (1976) 121–147.
- [42] D.E. Benteil. Aspects of Dynamic Pattern Generation in Embryology and Epidemiology, PhD thesis, Wolfson College Oxford, 1990.
- [43] D.E. Benteil, J.D. Murray, On the mechanical theory for biological pattern formation, *Phys. D* 63 (1993) 161–190.
- [44] J.D. Murray, G.F. Oster, Cell traction models for generating pattern and form in morphogenesis, *J. Math. Biol.* 19 (1984) 265–279.
- [45] G.F. Oster, J.D. Murray, A.K. Harris, Mechanical aspects of mesenchymal morphogenesis, *J. Embryol. Exp. Morph.* 78 (1983) 83–125.
- [46] A.K. Harris, D. Stopak, P. Wild, Fibroblast traction as a mechanism for collagen morphogenesis, *Nature* 290 (1981) 249–251.
- [47] V. Fleury, T. Watanabe, About the equilibrium shape of fibred structures, and biological shape, *C.R. Biol.* 327 (2004) 663–677.
- [48] P.L. Gould, *Analysis of Plates and Shells*, Prentice Hall, 1999.
- [49] H.C. Lee, R.E. Gaensslen, *Advances in Fingerprint Technology*, CRC Press, 2001.