Embryologic Development of Epidermal Ridges and Their Configurations

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The configurations of epidermal ridges that comprise dermatoglyphic traits are, in many respects, a history of the developmental period during which the ridges form. In 1892 Sir Francis Galton [1] demonstrated that epidermal ridge configurations did not change throughout postnatal life. The fact that ridge configurations were not affected by environment or by age has been an important framework in genetic studies. In 1936, Cummins [2] reported the association of unusual dermatoglyphics with Down syndrome. Confirmation of his findings [3-5] demonstrated the potential value of dermatoglyphics in clinical medicine. While not diagnostic alone, dermatoglyphics have been a valuable aid when clinical diagnosis was in doubt. Unusual dermatoglyphics now have been associated with congenital defects of both genetic and environmental origin [6]. Schaumann and Johnson [7] have noted that dermatoglyphics associated with congenital defects are significant markers of prenatal events. Yet, at present little is known about the atypical developmental processes that have produced these associations. The precise configuration of epidermal ridges and minutiae is determined at a very early embryonic age, around 10 weeks postfertilization. Accordingly, an understanding of the prenatal morphogenesis of dermatoglyphic traits is fundamental to our interpretation of their variation and their relationship to birth defects.

The developmental history of dermatoglyphic traits requires first a background in the normal developmental chronology of prenatal hand. Second, it includes an understanding'of the development of epidermal ridges, the basic building blocks of dermatoglyphic traits, and factors that may influence ridge configuration. The developmental basis of dermatoglyphic traits is fundamental to a better understanding of their variation and relationship to congenital defects.

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THE DEVELOPING PRENATAL HAND

Before discussing the prenatal development of dermatoglyphic traits, it is important to have an appreciation of the developing surface topography of the hand and foot, especially as to how surface changes correlate with subsurface cellular changes. This discussion will center on hand development. Development of the foot follows a similar chronology with the exception that foot development lags behind hand development by about 1 week.

During the 5th and 6th postfertilization weeks, the future hand becomes evident as a ventrodorsally flattened plate [8]. There is a progressive contouring of the margins of the hand plate such that the plate appears to have a crenated margin, signaling the appearance of fingers or rays. These rays correspond to the formation of mesenchymal thickenings or condensations within the hand. The mesenchymal condensations will develop into the skeletal and muscle components of the hand. During the 6th week, distinct finger rays and interdigital notches are seen. By 7 weeks, the mesenchymal condensations within the hand plate begin to differentiate into cartilaginous bone models and the external morphology of the hand demonstrates the continued formation of fingers as tissue between adjacent rays begins to disappear. During this period volar pads first appear on the volar surface of the palm. By 8 weeks, apical volar pads begin to appear, the distal phalanges of the hand have begun to ossify, and joints have begun to form between the bones of the hand. By 8.5 weeks the shafts of the metacarpals have begun to ossify and the hand has attained an external morphology similar in proportion to the infant [9].

VOLAR PADS

The development of epidermal ridges is preceded by the formation of localized eminences, volar pads, on the ventral apical region of the digits as well as on the interdigital, thenar, and hypothenar regions of the palms and soles. The importance of volar pads in the ontogenesis of epidermal ridges is that the pads are the site of epiderrnal ridge development. In addition, the configuration of epidermal ridges is probably influenced by the mechanical processes of growth of the pad. The volar pads are actually slight swellings of mesenchymal tissue.

Volar pads first appear as discrete elevations on the palm around 6.5 weeks postfertilization, followed on the digits by apical pads about 1 week later. The first volar pads appear over the 2nd, 3rd, and 4th interdigital areas of the palm. Other palmar pads follow shortly after

the first three. Apical pads are thought to follow a radioulnar gradient of development with the apical pad of the first digit appearing prior to the pad of the second digit, etc. [10].

Whipple [11] found that in addition to the primary volar pads noted above, secondary pads can be seen on the hands of adult primates. Cummins [10] noted similar secondary pads in the developing hand. Secondary pads are characterized in the human prenate by their short duration. Secondary pad refers primarily to a large elevation on the palm, first seen around 7 weeks and disappearing during the 7th week. In addition, paired swellings on the proximal phalanges have been reported between 8 and 9 weeks and a single pad at the base of the thumb has been found to persist to 10 to 11 weeks.

Between 6.5 and 10.5 weeks, volar pads exhibit rapid growth and in the palm individualization. Initially, apical pads appear to be all evenly rounded; however, by the 9th week, the pads begin to vary both in position and in shape. Palmar pads tend to demonstrate some individual variation prior to apical pads.

The primary pads start to regress after 10.5 weeks. This involution continues until pads are comparable in appearance to pads of the infant [10]. In the process of involution, variations occur both in the persistence of pads and in the shape of the pads. Cummins [10] noted the significance of pad regression and the initiation of epidermal ridge differentiation. In addition, recent embryologic studies have suggested that palmar, plantar, and digital creases develop concurrently with volar pads [12,13] rather than as a consequence of early flexion movements [14].

Volar pad development on the foot follows a similar chronology with the exception that volar pads of the foot lags behind the hand by about 0.5 week. A tibiofibular gradient in development is present. Regression of volar pads on the foot begins around 12 weeks.

DEVELOPMENT OF EPIDERMAL RIDGES

Numerous descriptive studies of epidermal ridge morphogenesis have been reported. Classical descriptions have been reported by Kölliker and others [15–21]. Additional studies on the origin of epidermal ridges have established that the critical period of primary ridge differentiation is between 11 and 17 weeks [22–24]. These findings on ridge development have been confirmed more recently by Blechschmidt [25], Penrose and O'Hara [26], Okijima [27], and Babler [28].

The initial regression of volar pads around 10–11 weeks corresponds to the initial formation of epidermal ridges. At this time the epidermis

is a smooth, thin layer of tissue both at the skin surface and on its deep surface at the epidermal-dermal junction (Fig. 1), and the surfaces of adjacent epidermal cells are already joined by strong desmosomes [26]. Epidermal ridges first appear as localized cell proliferations in the basal (deep) layer of the epidermis during the 10th week postfertilization (Fig. 2). These cell proliferations form shallow primary ridges that project into the superficial layer of the dermis (Fig. 3). The number of primary ridges increases as new ridges are formed between or at the lateral surface of existing ridges. Primary ridges proliferate rapidly to keep pace with the increasing separation of adjacent ridges due to general growth of the hand. This proliferation produces the branchings and islands, the minutiae.

The term "minutiae" refers to the details of morphology of a single ridge [23] and includes branchings, interruptions of the continuity of a ridge, and isolation of short ridge segments. Minutiae reflect the formation of new ridges subsequent to the period of initial ridge formation. Hale [23] was able to show that the tendency of ridges to multiply (and form minutiae) was greatest during the period of maximum difference between the increase in surface area of the hand and increase in ridge breadth.

As primary ridges begin to develop, they define the basic ridge configurations of the volar skin surfaces (Fig. 4). However, these configurations develop at the epidermis-dermis interface and not on the skin surface. As the number of primary ridges increases, the ridges continue to increase in dimension [28–30]. Primary ridges increase in width and penetrate deeper into the underlying dermis.

Around 14 weeks, sweat gland anlagen appear at uniform intervals along the apices of the ridges. The sweat gland anlagen, future sweat glands and their ducts, continue to elongate and penetrate deeper into the dermis. The association between primary ridges and sweat glands has resulted in the term glandular fold being used often in reference to primary ridge. The primary ridge, or glandular fold, corresponds to the surface ridge that we see.

At approximately 15-17 weeks, several key events occur in the ontogenesis of epidermal ridges. Around 15 weeks, the stratum corneum appears with the initial deposition of keratin on the surface of the epidermis. Secondary ridges, lacking sweat gland anlagen, also appear at this time (Fig. 5). Secondary ridges, or furrow folds, correspond to the furrow of the surface ridge. Concomitant with secondary ridge formation is the termination of primary ridge formation. Accordingly, by 17 weeks the human fetus has an epidermal ridge configuration that

Fig. 1. Histologic thin-section through the apical pad of the third digit of a IO-week fetus. Note the flat relief of the basal layer of the epidermis, stratum basalis, (B). P, periderm; I, stratum intermedium.

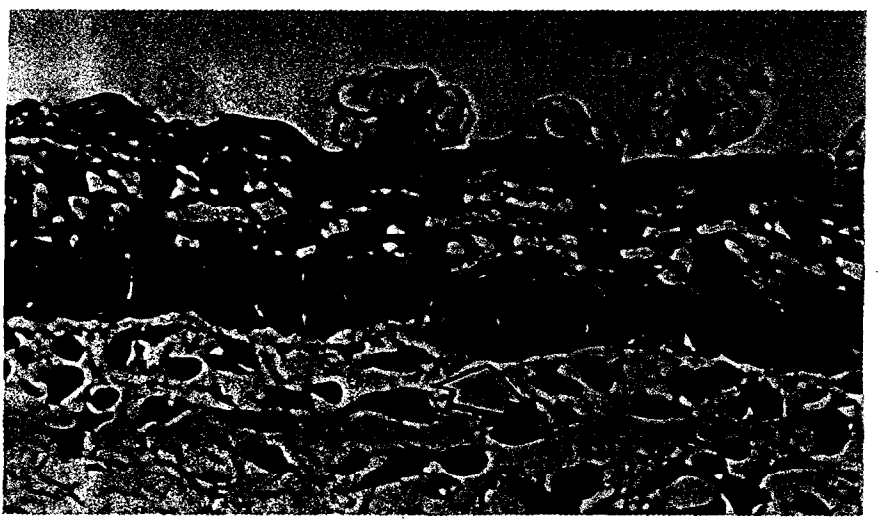

Fig. 2. Histologic thin-section through the volar pad of the third digit of a 10.5-week fetus. Note the localized proliferation of cells (arrow) in the basal layer of the epidermis. This is the initial formation of a primary ridge.

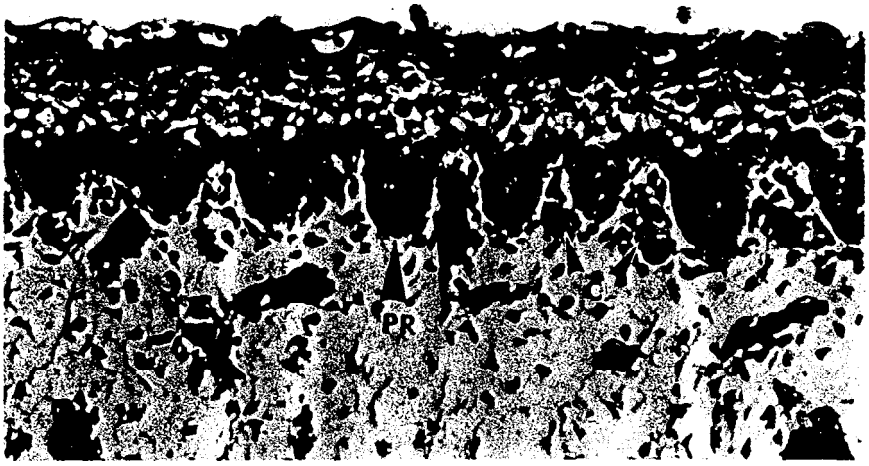

Fig. 3. Histologic thin-section through the volar pad of the third digit of an 11-week fetus. Note evenly spaced primary ridges (PR) projecting into-the underlying dermis and the relationship of capillaries (C) in the superficial dermis to the primary ridges.

is comparable to that of an adult. At the end of this period of time, epidermal ridges become visible on the volar surface as fingerprints.

From 17 to 24 weeks, secondary ridges continue to proliferate until they are in a one to one correspondence with primary ridges. It should be noted that secondary ridges develop in a manner similar to that of primary ridges, although only primary ridges have sweat gland anlagen associated with them. At 24 weeks, the epidermal ridge system has an adult morphology (Fig. 6).

Dermal papillae begin to develop around 24 weeks. Until this time the morphology of primary and secondary ridges is a smooth ridge of tissue. As the depth of the secondary ridges approximates that of the primary ridges, additional changes can be seen [29]. At this time bridging or anastomoses between primary and secondary ridges begin to appear. The dermis between anastomitic epidermal bridges progressively forms peg-like structures, the dermal papillae characteristic of the definitive dermal ridge.

The process of primary ridge formation is not a generalized event that occurs simultaneously across the volar aspect of the hand. Rather, ridge formation initiates at several points and spreads out such that developing ridge "fields" ultimately meet. The fingers are the earliest sites of ridge formation. Ridge differentiation spreads proximally from fingertip to palm and in a radioulnar (tibiofibular) gradient [29]. Ob-

Fig. 4. Histologic thin-section through the volar surface of the third digit of an 11-week fetus showing the configuration of epidermal ridges (ie, the darkly stained cells, arrow) as they project into the dermis. The plane of section is parallel to the volar surface.

servational data [18,21] suggest that on the finger, the center of the apical pad is the first region to demonstrate primary ridge formation. This is followed by the appearance of ridges along the distal periphery of the digit and subsequently by a field of ridge development, proximal to the apical pad. However, Hirsch and Schweichel [31] reported that ridge formation initiated along the laterodistal portion of the digit and proceeded in a proximomedial direction with the center of the pad initially being free of ridges. Once ridge formation begins, the number of ridges proliferate from these sites to meet adjacent ridge "fields."

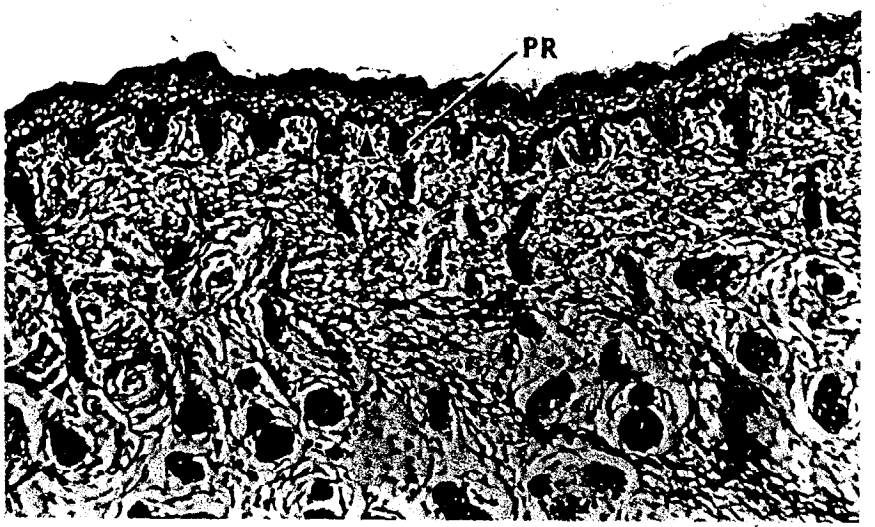

Fig. 5. Histologic thin-section through the volar surface of the third digit of a 17-week fetus showing the initial formation of secondary ridges (furrow folds), arrows. Epidermal ridges now are visible on the volar surface. Note the correspondence between the surface ridge and the primary ridge (glandular fold), **PR,** of the epidermal-dermal junction. Note also the sweat gland anlagen, SG.

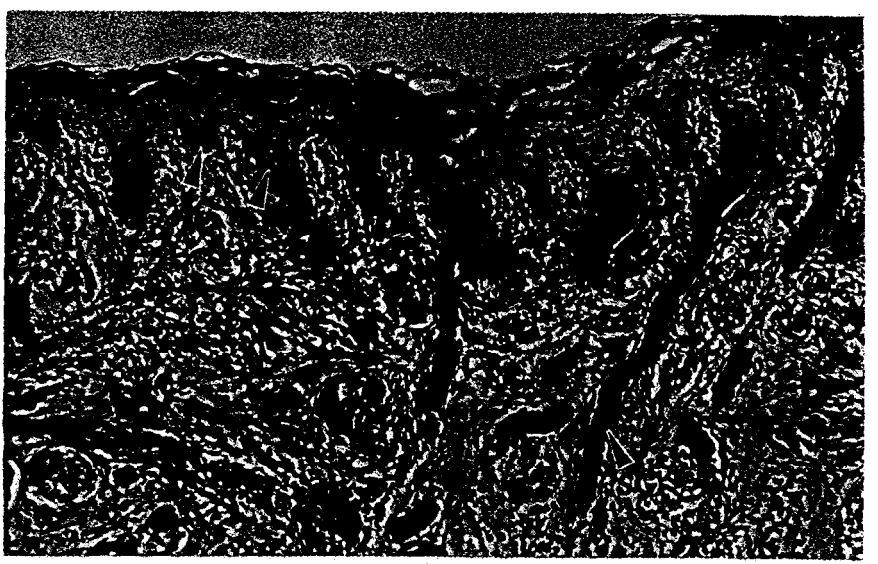

Fig. 6. Histologic thin-section through the volar surface of the third digit of a 21-week fetus, Note the increasing penetration of secondary ridges (furrow folds), S, and the continued penetration of sweat gland anlagen, SG, into the dermis. **PR,** primary ridge (glandular fold).

FACTORS INFLUENCING RIDGE CONFIGURATION

The factors that may influence ridge configuration are not readily identified. Yet, they are the keystones to understanding the biologic basis of variation in dermatoglyphic traits. Cummins [32] noted that "epidermal variants must be explained by a disturbance of germinal configuration determinants or by the admission of an immediate control of ridge direction which is not fixedly predetermined." While the genetic basis of dermatoglyphic traits has been well established, current research suggests that the genetic component of dermatoglyphic traits operates indirectly on ridge configuration through ontogenetic factors, eg, pad topography, growth rates, and stress on the epidermis, that influence ridge alignment.

Growth Stress

Kollman [22] was the first to examine the question of what determines the alignment of epidermal ridges. He suggested that ridge direction was greatly influenced by growth stresses and compressions in the developing skin. Penrose [33] extended this hypothesis to state that ridges align at right angles to the compression forces acting on the growing volar surface. This concept has received considerable attention from a mathematical perspective [cf. 34]. These include measurement of the curvature of epidermal ridges and their configurations [35].

Volar Topography

Bonnevie [36] first noted the correspondence between the height of a volar pad and the special ridge configuration of its pattern. She also proposed that differences in pattern type were related to variations in thickness of the epidermis and/or cushioning, a water-logged state of the epidermis. Hale [29] found that a critical thickness in the epidermis was indeed necessary for ridge morphogenesis to initiate but no evidence for cushioning. More importantly, he found that ridges formed not from a mechanical folding of the epidermis [17] but from actual cell proliferation.

Cummins [37], having observed the ridge configurations of congenitally malformed hands, proposed that direction of epidermal ridges was determined by growth forces and the contour of volar skin at the time of ridge formation. Wilder [38] likewise stated that inheritance of ridge configuration was "not a direct one, but rather one which results from its inheritance of the topography" of the volar areas. Mulvihill and Smith [34] synthesized data from a number of earlier workers to further develop the Cummins' topographic model for ridge configu-

ration. They stated that "ridge configurations are the immediate result of physical and topographical forces affecting the volar skin" during ridge formation. Therefore, ridge configuration is dependent on the shape of the volar pad at the time of initial primary ridge formation. A high, round pad would result in formation of a whorl while a low pad would result in an arch. An intermediate pad height offset to one side of the digit would result in a loop configuration.

Recently, Babler [39] has provided evidence to suggest that volar pad shape is indeed associated with ridge configuration. Although epidermal ridges are not visible on the volar surface until after the 17th week, Babler [28,39] used histologic techniques to reconstruct human ridge configurations at the epidermal-dermal junction 10 to 25 weeks postfertilization. Results of these studies indicated that the timing of primary ridge formation was associated with the type of ridge configuration. Early ridge formation was associated with a whorl-type of pattern. Late ridge formation was associated with an arch configuration and intermediate ridge formation with a loop. Since apical volar pads initiate their involution around 10.5 weeks, the relative degree of pad regression at time of ridge formation apparently is associated with ridge configuration. Additionally, Babler [40] reported that rather than pad height being a key factor in ridge configuration, pad width relative to height was the associated factor. These data also provide developmental evidence to support Abel's hypothesis [41] that pad elevation had no effect on the number of ridges. Abel had noted that populations with different frequencies of pattern types had similar numbers of ridges measured from a pattern core to the lateral nail fold. Babler [40] was also able to demonstrate prenatally a direct association between apical pad symmetry and loop direction (ulnar or radial).

Neurotrophic Factors

Bonnevie [17] suggested that there was a direct relationship between cutaneous nerve distribution and the location of the centers of ridge patterns. Hale [23], however, found no evidence to suggest a trophic interaction between peripheral nervous elements and the basal cells of the epidermis. Blechschmidt [25] proposed that the vascular patterns of the volar surface determine ridge configuration. Hirsch and Schweichel [31] using electron microscopy reported the regularity of spatial relationship between capillary-neurite pairs and dermal ridges. They felt that primary ridge formation was induced by vessel-nerve pairs subjacent to the epidermal-dermis junction. Accordingly, the spatial arrangement of vessel-nerve pairs at the time of primary ridge formation directly influenced ridge configuration. Recently, again using

EM techniques, Dell and Munger [42] supported a role for sensory axons in modulating ridge formation, confirming Bonnevie's initial hypothesis. Further, they believe that some degree of the variability in ridge configuration is due to the overlapping of dermatomes. Therefore, there is mounting evidence that the neuroepithelium does play an important part in epidermal ridge development.

Ridge Bundles

Recently, de Wilde [43] suggested that ridge configuration was determined long before ridges actually appear at the epidermal-dermal interface, during the fifth and sixth week. This requires that ridge configuration be determined before the separation of the digits, during the hand plate stage. This precludes the role of volar pad topography in influencing ridge configuration. He suggested that the topography of the volar pad may actually be determined by ridge configuration. Further, ridge configuration on digits must be determined prior to formation of interphalangeal and metacarpophalangeal creases. Within this hypothesis ridge configuration involves common developmental fields, or ridge systems, for the hand that secondarily is subdivided into digits. After separation of digits, ridge "bundles" develop in a radioulnar sequence to invade the palm from interdigital regions. What factors could influence ridge configuration long before ridges initially develop is unclear. Work by Elsdale and Wasoff [44] suggested that one answer may be cell behavior. They reported that in vjtro fibroblasts typically align in parallel fields and display a pattern topology. Similar findings for cultured human epidermal cells have been reported by Green and Thomas [45]. While de Wilde's hypothesis has several points of contention, eg, the thumb ray does not initially develop adjacent to the remaining finger rays, it underscores two important points. First, ridge configuration probably is influenced by factors acting prior to epidermal ridge formation. As early as 1929 Bonnevie [18] suggested that factors that influence ridge configuration such as thickness of the epidermis may, in many cases, **have** existed prior to separation of the digits. And second, **cell behavior may play some role in ridge configuration.**

Skeletal Factors

Abel [41] first showed a direct relationship between number of ridges and length of the distal phalanges in adults. He suggested that both were independent of pattern type and size. Gall et al [46], in discussing the Holt–Oran syndrome, expanded on this association to suggest that ridge configuration itself reflected the patterns of development of growth centers of the hand itself. Recently, Babler [40,47] has examined the

developmental relationships between epidermal ridges and the developing bone skeleton of the hand. He has shown a significant prenatal relationship between epidermal ridge dimension and bone dimension of the hand. Bone dimensions, both in length of the cartilaginous model and bone collar, of distal phalanges and metacarpals were significantly correlated to digital epidetmal ridge dimensions. Specifically, bone lengths but not widths were significantly correlated to the amount of separation between adjacent primary ridges during early fetal growth. Shape of the distal phalanx has a significant association with pattern type. Similarly, when fetuses were matched for the relative degree of ossification of bones of the hand, length of the distal phalanx was associated with pattern type. Whorl patterns tend to be associated with shorter distal phalanges. Relative degree of ossification of the bones of the hand has an association with ridge configuration. Whorl patterns tend to be associated with less ossification, suggesting either early ridge development relative to bone maturity or delayed bone development relative to ridge formation. Generally, we can conclude that bone development does play a role in epidermal ridge configuration.

DISCUSSION

Recent work in prenatal dermatoglyphics has begun to apply our increasing understanding of epidermal ridge development to a better understanding of congenital defects. Generally, these applications can be subdivided into three areas: prenatal dermatoglyphics, epidermal ridge growth, and developmental perspectives of postnatal dermatoglyphic differences.

Prenatal Dermatoglyphlcs

Since the basic pattern of ridge configuration is determined as the first primary ridges appear, methods to' study the "fingerprints" of young fetuses are currently being used to better understand the biologic foundation of variation in dermatoglyphic traits. In a study of human fetuses derived from either spontaneous or elective abortions, Babler [39] reported evidence of prenatal selection associated with digital dermatoglyphics. He found that spontaneous abortuses free of gross or chromosomal defects and with no confirmed clinical indication of abnormality had a significantly higher frequency of arches than "normal" fetuses derived from elective abortions. In a separate study of a group of various abnormal fetuses, Babler [48] reported a significantly higher incidence of arch patterns on the digits.

Suzumori [49] used the techniques of Okajima [27] to study the

dermatoglyphic features of human abortuses with chromosomal abnormalities. His observations suggest that the developmental sequence of ridges with chromosomal disorders was retarded by more than two weeks as compared to age-matched normal fetuses.

Epidermal Ridge Growth

From the initial appearances of primary ridges around 11 weeks, prenatal growth of primary ridges can be divided into three basic components: (1) width of the primary ridge, (2) amount of penetration (depth) of the ridge into the dermis, and (3) spacing or separation between adjacent primary ridges. Babler [28] demonstrated significant population differences in the growth of specific epidermal ridge dimensions of both elective and spontaneous abortuses. Furthermore, he has shown that spontaneous abortuses had significantly less growth in primary ridge depth when matched for age [30]. No significant differences in other ridge dimensions were observed. The dimensional differences between elective and spontaneous abortuses are important for two reasons. First, ridge depth is a ridge dimension that cannot be measured on the skin surface. Therefore, this is a soft tissue difference not previously noted. Second, there are some data to suggest an association between pattern type and ridge depth [28]. In developing fetuses, a whorl pattern tends to be associated with an increased ridge depth while an arch pattern tends to be associated with less ridge depth. As noted above, fetuses that spontaneously abort tend to have a higher frequency of arches than those aborted electively.

We can also use dimensional growth of epidermal ridges as a screening tool in examining abnormal or potentially abnormal fetuses. As shown in Figure 7, primary ridge width tends to be linearly related to crown-rump length, a good estimator of prenatal age, during the second trimester. Included are the 95% confidence limits (dashed lines) of an individual. Also shown are the relative position of a series of abnormal specimens. Note that the widths of both Down fetuses fall below the 95% confidence limits as does the width of a fetus exposed prenatally to rubella. Both of these abnormalities have atypical dermatoglyphic traits associated with them [6]. Interestingly, two of three fetuses with cleft lip and palate (CLP) fell outside the confidence limits. The association of atypical dermatoglyphics with cleft lip and palate is not established. These data suggest there may be at least some dimensional effects on epidermal ridges associated with congenital defects not previously recognized.

Differences between spontaneous and elective abortuses in maturation of epidermal ridges have also been reported [30]. Spontaneous

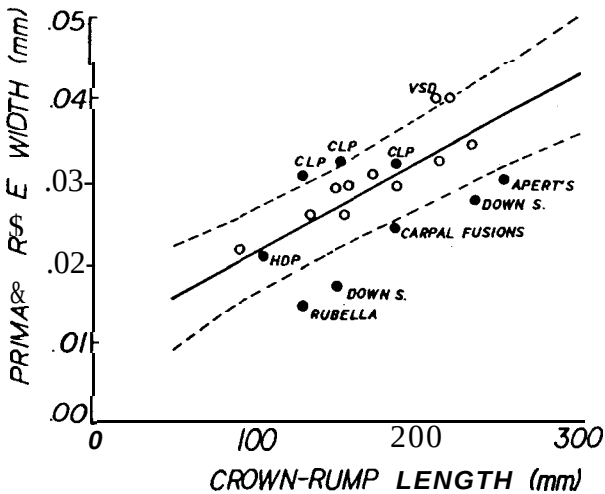

Fig. 7. Linear regression line of primary ridge width versus crown-rump length with 95% confidence limits (dashed lines) for normal fetuses. Primary ridge widths of individual "abnormal" fetuses are plotted relative to the norm. Note two Down syndrome fetuses as well as a rubella-exposed fetus lay below the confidence limits. CLP, cleft lip and palate; HDP, hypoplasic distal phalanges; VSD, ventricular septal defect.

abortuses exhibit a delay in ridge maturation relative to age-matched elective abortuses.

Developmental Approaches to Understanding Dermatoglyphic Differences

It has become evident that the dermatoglyphic traits seen postnatally realistically reflect the shape and developmental history of the hand during early fetal and possibly embryonic life. Increasingly, dermatoglyphics have been used as a measure of prenatal development. Asymmetry in dermatoglyphic traits has been used as a measure of developmental "noise" [50, 51]. Meier et al [52] have used the developmental basis of dermatoglyphics as a tool to examine postnatal maturation. Rose [53] has reported an association between the presence of 10 digital whorls in women having histories of multiple spontaneous abortions. The potential inductive role of sensory nerves in ridge formation may suggest a common developmental basis for nerve aplasias or disturbances of dermatotopic patterns anddysplasias and aplasias of epidermal ridges. The association of ridge configuration with aspects of bony development within the hand suggests that ridge configuration may be influenced as early as the initial stages of bone formation, ie, prior to ridge formation. Many quantitative measures of dermatoglyphics in-

volve the counting of ridges. Yet we may ask what does a ridge count measure? Increasing prenatal research now allows us to address the biologic basis for their variation. Finally, since epidermal ridges reflect the developmental interaction at the epidermal-dermal interface, specific differences in epidermal ridge development associated with dermatoglyphic differences suggest that ridge configurations may contain more developmental information than is currently recognized.

CONCLUSIONS

Our emerging understanding of the developmental origins of dermatoglyphic traits requires that we now view dermatoglyphics as a living history of prenatal development. Epidermal ridge configurations not only offer useful information on early hand morphology, but have the potential to be useful prenatal markers of variations in development of the innervation, skeleton, and soft tissues of the hand. Our evolving understanding of the epidermal ridge development will greatly expand our understanding of the developmental factors that may produce congenital malformation.

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