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Dr. Radomír Čihák, DrSc.,
Department of Anatomy,
Charles University Medical Faculty, Prague

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I. Introduction

The aim of the present publication is to summarize the results of studies of ontogenesis of the skeleton and muscles of the human hand and foot. Our primary interest in studying the muscles arose from observations of variations, in which a new form of the anomalous muscle in the popliteal fossa had been described (Čihák, 1954; Hněvkovský and Čihák, 1957) and in which changes of muscle forms in the congenitally malformed extremity had also been studied (Brůčková and Čihák, 1956). The desire to clarify muscle variations by means of the ontogenesis led to a study of ontogenesis of single muscles. During observation of the embryonic pectoralis major special muscle bundles were primarily observed, which could be homologised with the sphincter colli muscle of lower Mammals. Further observation revealed that this muscle (concordantly with its phylogenetic development) gradually develops in the course of human ontogenesis from a small primordium to its maximal extent and becomes reduced thereafter and finally disappears, still during the embryonic period (Čihák, 1957). This study was decisive for the further development of our theme, since it demonstrates, how consistently in the development of the locomotor apparatus the rule of recapitulation is asserted and how this can be employed in developmental studies of muscles. It was therefore presumed that the more complicated morphogenesis would be found in the course of the embryonic development of muscles undergoing more complicated changes of their external shape during phylogenetic development. For the subsequent developmental studies, therefore, the muscles have been selected according to the differences of their morphology in Mammals of various phylogenetic levels, e.g. some spinohumeral and thoracohumeral muscles. The studies brought about a number of results: five developmentally independent components of the pectoralis major were found in human ontogenesis, later fusing to form the typical pattern of this muscle (Čihák, 1959, 1960a); the typical ageneses of the pectoralis major were found to be mosaic-shaped defects occurring exactly according to single embryonic portions of muscle (Čihák and Popelka, 1961). The determination of five fundamental portions of the pectoralis major in human ontogenesis became the basis for the homologisation of the complicated pectoralis musculature in the comparative anatomy of various mammalian orders (Štěrba, 1967a, 1968a). The latissimus dorsi and its two components have similarly been studied (Čihák, 1960a, 1963a). In the course of the development of the latissimus dorsi also the dorsoepitrochlearis muscle was repeatedly found in young embryos (Čihák, 1961, 1963a). Contrary to this, the distinct portions of the trapezius muscle, which have been claimed to exist in adults, were never found in embryos and they appear as a secondary pattern (Čihák, 1960a); this view has been revised and supported from the comparative standpoint by Štěrba (1965, 1967b, 1968b) and by Štěrba and Berg (1963). In the development of the human deltoid muscle a similar result was obtained concerning its claviculo-acromial part by Hořejší (1968). The later description of the interesting muscular anomaly—the musculus sterno-cleidomandibularis—in man and an attempt at its developmental explanation also belongs to this group of studies (Hněvkovský and Čihák, 1967). In the lower limb a developmental independence of components of the quadriceps femoris was found (Čihák and Puzanová, 1960). The developmental recapitulation of changes in form in the deep portion of the masseter and in the corresponding region of the mandible was also encountered (Čihák and Vlček, 1962).

During this first step of our studies valuable experience was obtained, revealing the existence of changes of the external form of muscles in a relatively late foetal period. It was possible to employ the standpoints of the comparative anatomy and the findings in the teratology and to combine it with the information concerning the embryonic development of muscles, and to continue in this manner the fundamental embryological studies, which from the beginning of this century dealt mainly with the early development of muscles. We soon recognized the necessity to keep muscular components in view and to consider their independence according to the form of the neurovascular hila, as described by Brash (1955). On this basis it was possible to demonstrate that many muscles developed during ontogenesis by fusion of originally independent elements, such muscles being at first a group of fully separate individuals and later a system of relatively independent components which each have their own nerve. From this standpoint the anatomical nomenclatorial usage, expressing the individuality of the muscle also by its name, is not always in accordance with reality, and this is to be taken into account when homologies are considered. The detailed knowledge of muscle components permitted clinical applications: it was possible, also in adults, to separate such a developmentally independent and separately innervated component and to employ it for the replacement of a paralysed function of another muscle (Čihák and Eiselt, 1962; Čihák and Hněvkovský, 1963).

After the above mentioned experience in the studies of developing muscles and muscle components it was possible to start studying an interesting and complicated muscle group—the intrinsic hand muscles.

There has been up to now only a fragmentary knowledge of the ontogenesis of hand muscles, with many contradictory points between the embryology and the comparative anatomy. Therefore, we tried primarily to assess the typical layers of the intrinsic musculature and their homologies. It was also found that the first dorsal interosseus originates by fusion of two neighbouring components corresponding to the so-called flexores breves profundi muscles of lower Mammals (Čihák, 1960b). An attempt at explaining (in the same paper) the origin of the three other dorsal interossei by the same mechanism was, however, incorrect, and was revised in subsequent studies (Čihák, 1963b, c, 1967a), in which the homologies of deep layers of hand musculature primordia (giving rise to the interossei) were established. In addition, in the embryonic human hand a layer of muscular primordia was found corresponding to the four contrahentes muscles of lower Mammals (Čihák, 1963b, c). Later on, the origin, extent and a special type of extinction of a part of this layer was observed in the hand (Čihák, 1967a, b, 1968a, b) as well as in the foot (Čihák, 1969a, c). The above quoted observation of fusion of the first dorsal interosseus from the two parts permitted the surgical reconstruction of thumb opposition by means of intrinsic hand muscles (Čihák, Eiselt and Fleischmann, 1963).

The revision of the disposition of primordial layers in the hand enabled further collaborators to extend the studies to the development of further muscles, e.g. the flexor digitorum superficialis which in the embryo is originally a hand muscle (Dylevský, 1967, 1968a, c), to the development and the spacial relations of the palmaris longus muscle and the palmar aponeurosis (Dylevský, 1968b, 1969a, c). The pattern of the layer of contrahentes muscles and of their embryonic primordia was examined in the rat (Trnková and Dylevský, 1969); the embryonic primordia of the interossei in rats were studied and the dorsal components of the interossei, typical of many Mammals, were found in rats to disappear during the course of embryonic development (Dylevský and Trnková, 1969). The study of the intermetacarpal space in chick embryos revealed the constancy of development of typical muscular primordia (known in Mammals) even in the intermetacarpal space of the extremely specialized Sauropsid extremity (Dylevský, 1968d).

In the developing human hand, moreover, further muscular and connective tissue components were observed. The accessory primordia of the dorsal interossei were described (Čihák, 1963c, 1967a, 1969c) and their persistence in adults was observed (Chmelová, 1963). Also the differentiation of the retinaculum flexorum and its relations to the developing skeleton and thenar musculature were observed (Čihák, 1966b, 1969b, c), as well as the clinical significance of anomalous muscles on the dorsum manus (Lunda and Čihák, 1967) and the phylogenetically ancient pattern of tendons of the embryonic extensor digiti minimi (Kaneff and Čihák, 1970).

Many principial points of the studies quoted are summarized as a basis of the present publication. During studies of extremities a question arises concerning comparisons of the upper and lower limbs. The study of developing muscles of the foot and the comparison with the hand is, therefore, one of the main themes of this paper. The further, non-subsidiary theme concerns the development of the hand and foot skeleton and its relationship to the developing musculature, since preliminary observations suggest that the developing skeletal elements also bear many phylogenetically ancient features (similar to developing muscle primordia) which permit developmental explanations. In considering the development of skeletal elements of the hand and foot the problem of their comparison and homologues cannot be overlooked, since there are many contradictions concerning this point even in relatively recent literature.

The present publication therefore examines step by step the development of the skeleton and of single muscular groups in the human hand and foot. The extent of the chapters and the different partial subjects do not permit the employment of the conventional simple scheme of the paper, with the final discussion and conclusions regarding all points after all observations at the end of the paper. It is necessary, for the sake of clarity of this paper, to proceed according to thematic chapters and to provide each with the given question, its solution and conclusions. Single themes are supplemented by the comparison of corresponding pattern in the hand and foot.

II. Material and Methods

During the many years of work on this subject, 373 series of human embryonic hands and feet were collected. This material contains 270 histological series of hands of human embryos and foetuses from 10 to 100 mm in crown-rump length. Most of them are transversally sectioned; for control the remaining series were sectioned either sagittally or parallel to the palm. The further material contains 103 series of feet of human embryos and foetuses from 15 to 90 mm C-R length, sectioned again transversally, sagittally and parallel to the sole. A series of embryonic hands of various mammals was also employed for comparison. From this entire material partial collections of 50–80 series were picked out for studies of single problems. The selection for those single studies from the entire material was always performed individually so that basic comparable stages of development have been repeated in all single studies and, moreover, so that the maximal number of series employed has belonged to the time of maximal morphogenetic changes of studied pattern (according to the range of their C-R lengths). It was thus possible to study the detailed sequence of development. The material extends to foetuses of such a size that no further changes in external muscle forms and in skeletal pattern can be observed, where the basic ligamentous and fascial structures are also formed, hence where the foetal hand and foot are closely similar to those of the adult.

The choice of material for individual partial series will be referred to in the subsequent text, always in front of the respective chapters. The number of series employed in partial studies (50–80 series) has made a sufficiently detailed examination of the developmental process possible. It was, therefore, not necessary to imagine the course of developmental changes between two remote stages, as commonly done in the papers of previous authors. We note for orientation that Ruge (1878a) performed his study on four foetuses (23, 35, 40 and 100 mm in length) and Windle (1883) also on four foetuses (24, 50, 70 and 120 mm). Gräfenberg (1905/06) does not indicate the number of his specimens, but it could be deduced from his text that he had 1–2 foetuses per week, from the fifth to the thirteenth foetal week; however, his descriptions do not correspond with the respective weeks according to the degree of differentiation. Bardeen and Lewis (1901) had 13 embryos; from this number they reconstructed six embryos. McMurrich (1903) illustrated his conclusions by one foetus of 60 mm, where, however, the developmental changes concerned took place a long time previously. Really extensive embryonic material appeared first in papers by O'Rahilly (1954), O'Rahilly, Gray and Gardner (1957) and Gray *et al.* (1957).

Due to the fact that in the critical stages of morphogenesis the C-R lengths of our material increase by half of a millimetre or one by one millimetre and that there are mostly a number of specimens of the same size, the continuity of the C-R length sequence represents a simultaneous control. By comparison of successive stages it can be demonstrated that no deviation from the form sequence occurs such as would signalize an anomaly. Such certainty is also supported by the fact that most of our series were obtained from the termination of normal pregnancies. This material was of two kinds: in one part of it the C-R lengths were preserved and it was hence possible to measure the embryo exactly; in the second part of the material, the C-R length could not be measured. Therefore our collaborator Dr. Ivan Dylevský employing the collection of undamaged embryos worked out a method of estimating the C-R length by means of external dimensions of extremity parts or by means of skeletal stylopodial or zeugopodial dimensions (by measuring and correlating lengths of extremities with other body dimensions — Dylevský, 1965, 1969b). This method enables us to assess the C-R lengths of the incomplete material from terminations.

Preparations studied by means of the stereoscopic microscope were used very little in this work, only for controlling the comparative material of hands of the following Mammals: Ornithorhynchus, Didelphys, Erinaceus, Nycticebus, Galago, Lemur, Hapale, Macaca, Pan, Gorilla (foetus). Comparative data were also taken over from the literature.

During processing histological series the question of staining the slides arose. In embryonic material which had frequently been preserved in formol for many years before processing there were difficulties in differentiation of very early myoblasts by the usual staining methods. Held's molybden hematoxylin which has suitable qualities for the simultaneous staining of various tissues was therefore selected. Later on this stain was modified with respect to the differentiation of muscle and connective tissue by applying the well soluble phosphomolybdic acid instead of the molybdic acid of Held's original formula (Čihák, 1963b, c). Staining with the thus modified Held's hematoxylin was useful for the old formol preserved material. The dye partly differentiated the early myoblasts in a dark violet to blackish tone from surrounding mesenchymal cells, partly stained all cellular processes, all membranes etc. in a very good and contrasting picture. In more advanced specimens the connective tissue can also be distinguished by the stain. By employing phosphomolybdic acid we obtain the components of connective tissue—especially if the collagen is already formed—in a red tone, well differentiated from that of future muscle cells. Moreover, the described method also stains the axons of peripheral nerves. This method was very suitable for the demarcation of early muscular blastemas in young developmental stages; on its basis the drawing of slides for plastic reconstruction was easily possible. The method, however, is not completely suitable for cytological purposes because of the lack of clear contouring of intracellular structures. We therefore changed this method later for staining with Ehrlich's hematoxylin, alone or with eosin, and still later for staining with Weigert's hematoxylin and eosin. This method yields the best results in the embryonic material, assuming that the material has not been fixed in formol for too long a time.

Some of the series were reconstructed. In two series of hands (embryo 15.5 and 21 mm in C-R length) the muscle primordia with the skeleton were completely reconstructed; from one series (embryo 28 mm in C-R length) the reconstruction of important parts of hand skeleton has been performed. The method of Born was employed for the reconstructions. The drawings were performed either by use of Abbe's apparatus, or from microphotographs with simultaneous microscopic control of the specimens, or directly from the microscopic slides projected on the paper. For the proper technic of reconstruction a plastic material known by the name of Modelit (produced by the firm Rohoplast, Prague) was employed in place of the wax normally used. This white material, based upon mixing pulverized PVC with organic softeners of the phthalate group, is used in schools as material for modelling. Modelled while cold, this material hardens without change of form and with only a slight change of volume into a white ivory-like matter on heating to 100–120° C. We worked in three steps:

1. The mass was rolled to the calculated thickness in a normal manner by a roller warmed to 40–50° C which made the mass smoother. While rolling the mass was dusted with talc so that it did not stick to the base or to the roller.

2. The rolled plates were warmed in the thermostat to 70° C for 5 minutes. After cooling down the material became slightly firm of approximately rubber consistency and could be well cut without adhering to the knife and without deformation. Drawings were copied on plates so prepared and cut out.

3. After mounting the reconstruction, and working its surface by apposition and subsequent modelling of fresh mass between the steps of reconstruction layers, the finished reconstruction was heated in the thermostat to 100–120° C for about five minutes per centimetre of object thickness; then the reconstruction was cooled down slowly in the thermostat.

There are several advantages of employing this new plastic material as compared with wax: its minimal combustibility, working in the cold, cleaness of working, easy surface modelling, hardness and durability of the reconstruction (Čihák, 1963c, 1966a). All these advantages fully compensate for the rather tiresome rolling. Besides Born's method graphic reconstructions have also been employed for detailed points of series. During studies of muscular primordia the reconstructions served mainly for improved spatial comprehensions. The reconstruction, at least a graphic one, was necessary for studies of the developing carpal skeleton since only on its basis could the really independent or the fusing parts of primordia be recognized.

We are aware that slight inaccuracies may accrue especially from surface modelling; the main contribution of the reconstruction, however, the plastic illustration of the observed pattern and the exclusion of errors in continuity or discontinuity of elements observed in histological series, fully counteracts the minute technical imperfection. We therefore avoided figuring patterns on the object surface which cannot be exactly revealed by the reconstruction, e.g. the direction of muscle fibres, surface details etc. The reconstructions, worked out minutely in this respect by Bardeen and Lewis (1901) and by Lewis (1901/02), carry significant traces of artificial modelling, based naturally upon adult muscle. This gives their reconstructions an appearance of structures more advanced than we find in our specimens, and than they are actually.

III. Ontogenesis and Homologies of Human Carpal and Tarsal Components

1. Problem of Development of the Carpus and Tarsus. The Morphology of Carpal and Tarsal Elements

The question of the origin, derivation and homologies of carpal and tarsal components has been an onerous problem in developmental anatomy for more than a hundred years. Interest was evoked by the work of Gegenbaur (1865) where the structure of the tetrapod extremity was derived for the first time from the fin of elasmobranch fishes. In the course of the subsequent development of the problem this idea was gradually exactified and geometrised (Gegenbaur, 1870a, b, c, d). Less known in the history of the problem, but quite important for later views on the development of the extremities is Gegenbaur's consideration of the uniserial "archipterygium" as the elemental extremity type, presented in these early works. From the archipterygium he derived the five-toed extremity so that he at first located the main axis through the radius and the fifth finger and derived the remaining fingers as collateral rays (Fig. 1A). Later on, influenced by Huxley's criticism (1873), Gegenbaur (1876) transposed the main extremity axis into the ulnar margin of the uniserial archipterygium and other fingers again were derived in the form of collateral rays.

In the meantime Gegenbaur (1873) established his famous, now already abandonned "theory of the archipterygium" where on the basis of Günther's (1871) he considered the pattern of the biserial Ceratodus fin, claimed this biserial archipterygium to be the initial form, derived the uniserial form from it and from this again by the above established process, the five-fingered extremity. From this original work of Gegenbaur, however, the questions of the comparison and homologies of carpal elements still remained topical and unsolved.

The basis for all subsequent considerations therefore became the pattern of the primitive carpus and the number of its elements as stated by Gegenbaur: three elements of the proximal row—the radiale, intermedium and the ulnare; two centralia—the radial and the ulnar one; five distal row elements, ossa carpi (distalia) I—V (Fig. 1A). These elements, declared by Gegenbaur to be constant, were then called by Braus (1906) canonic elements, to point out their distinction to additional accessory carpal components. (It will be pointed out later that much more constant elements were established subsequently.) According to Gegenbaur the elements in the primitive carpus are assembled symmetrically to the third digit; however, the line set through the autopodial margin represents the original main axis of the biserial and uniserial archipterygium.

At that time also in connection with Gegenbaur's general idea of extremities, carpus and tarsus, a series of works appeared applying or varying in detail this concept of carpal and tarsal elements in comparative anatomy and in embryology as well as in human anatomy and variability (Fürbringer, 1870; Wiedersheim,