EVOLUTION OF THE HAND

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There was an ape in the days that were earlier, centuries passed, and his hair become curlier, centuries more gave a thumb to his wrist – Then he was man and a positivist

(Edward James Mortimer Collins –The British Birds. A communication from the Ghost of Aristophanes)

Humans and other primates live what might be called a 'hand to mouth' existence. In contrast to most of the non-primates whocarry their mouths to the food, primates carry the food to their mouth. In the process of evolution such fundamental differences in behaviour are accompanied by some notable anatomical like migration of eyes to front of face, shortening of the snout and prehensility of the hand.

The human hand evolved from a specialised fin 400 million years ago, and the multiple shapes and purposes have culminated in a masterful instrument capable of greater skill and a source of great despair.

Origin of ideas and contribution to hypothesis

Origin of ideas started far back in the minds of natural scientists in the nineteenth century who observed phenotypic features of human hand limb compared with those of other primates and mammals.

Sir Charles Bell in his famous essay, the Bridgewater Treatise, commented on the unique perfection of human hand in its full array of possibilities as compared with analogous structures in Chimpanzees, the horse and the birds.

Although Charles Darwin in his Origin of Species(1859) explained regarding the survival of the fittest after observing insects and animals for decades, it was not until The Descent of Man(1871), that he published his daring observations on the origin of Homo sapiens.

Ernst Haeckel's controversial concept of "ontogeny recapitulates phylogeny", meaning that the evolutionary history of species is seen in early development but fades towards adulthood, introduced the concept that our ancestors had amphibious gills and tails just like embryonic humans. His observations contributed to a continuum of modern evolutionary theory that begs one more hypothesis: *that every congenital hand anomaly has an evolutionary cognate(Fig 1).*

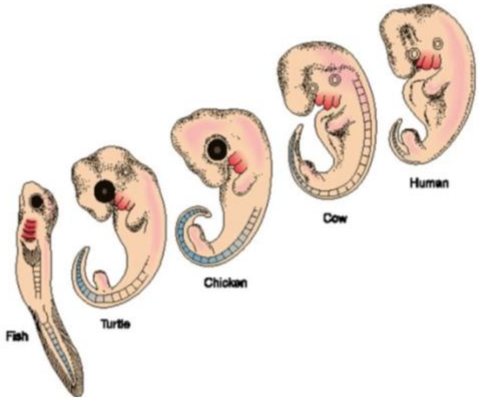


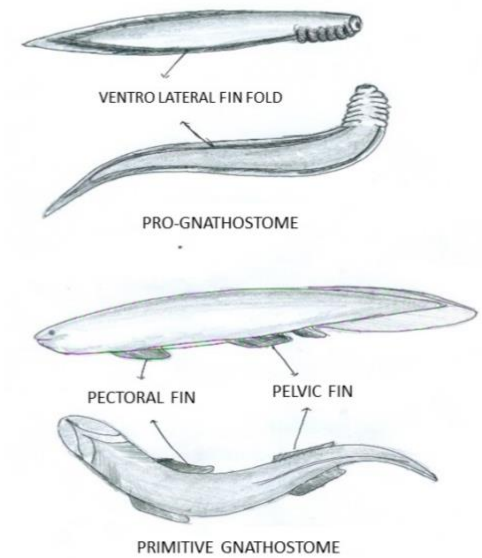
Fig 1. Embryos of different vertebrates share basic primitive features such as gills (red) and tails (blue).

John Napier, a surgeon and primatologist whodescribed Homo habilis as first 'Handy man', described the hand as "the single most crucial adaptation in our evolutionary history." Our hands helped to make things possible like use of tools, language development, the enlargement of our brain, and even human culture.

Origin of paired appendages – Fin to Hand theory:

The paired appendages originated400 million years ago. Two theories were proposed regarding the evolution with much of controversies between morphologists. The lateral-fin theory has supplanted the much famous gill-arch theory of Gegenbaur and is now accepted as the most plausible explanation of the beginning of these appendages [3].

According to lateral arch theory, the paired appendages are derived from longitudinal lateral folds of epidermis extending backwards along the body from just behind the gills to the anus. By accentuation of anterior and posterior and suppression of intermediate portions of folds the pectoral and pelvic fins were formed (fig 2).



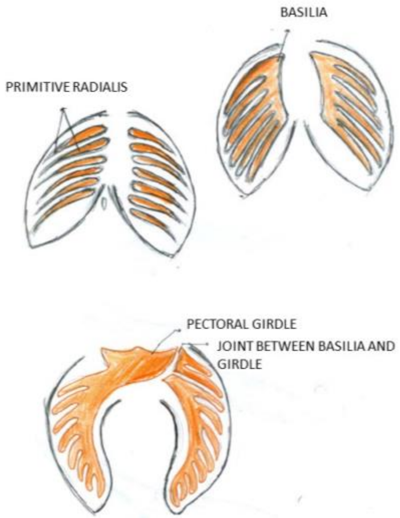


Fig 2.Hypothetical representation of vertebral fin fold and its derivatives. Drawing adapted from Jarvik, 1980.

Fig 3. Hypothetical representation of development of pectoral girdle.

Muscle buds from the ventral border of adjoining myotomes migrate into these folds giving rise to radial muscles which help in movement of the fins and were forerunners of intrinsic muscles of hand. They derive their nerve supply from the ventral roots of spinal nerves. Peripheral nerve fibre in the base of fin divide repeatedly giving rise to complex plexus. In ontogeny, motor nerve always supply the muscle for which they were originally designed. Muscle exhibiting dual nerve supply denote combining of muscular tissue of several segments.

Next in the process of evolution of appendages was the appearance of radialis (cartilage rays) between the muscle buds, these provided more strength and support to the fins. Fusion of proximal ends of radialis in fin give rise to basilia which extend into body wall and fuses with the opposite side in midline centrally to form more primitive pectoral girdle. Later with the demand of greater mobility of fins a joint appeared between the radialis and basilia, which in turn articulate with the girdle (fig 3). The primitive girdle consists of ventral segment coracoid and dorsal segment scapula which on further segmentation by the appearance of spine process resulted in supra and infrascapular segments to accommodate greater muscle mass for shoulder mobility.

Further in evolution of pectoral girdle is the appearance of membranous bone derived from skin. Each half of membranous circle consist of 4 membranous bones; 1) post temporal which is joined with skull there by resultingin gross restriction of freedom of movement 2) supraclethrium 3) clethrium and 4) clavicle.

The changes from aqueous to a terrestrial existence was accompanied by pronounced alteration in the skeletal elements of the pectoral fins which were now used for support and locomotion. The post temporal and supraclethrium part of membranous bones disappeared,thereby freeing of limb from skull resulting in increased freedom of locomotion.

Coracoid process which was large in amphibians usually connected across the body to opposite pectoral girdle there by decreases the freedom of movement of fore limbs. During evolution from amphibians to mammalians, in order to increase the arc of movement of shoulder, there was progressive regression of coracoid to remain as small process in humans. At the same time clavicle developed and became progressively larger in size. With its only ligamentous connection to the axial skeleton and scapula the arc of rotation at the shoulder is increased.

The proximal element was destined to become the humerus, middle elements the radius and ulnar, the distal elements the carpus and the digits. The principal element in the radial side became the thumb, and those on ulnar side became four digits, pentadactyly limb which was maintained in all stages of evolution up to and including man. (Fig4)

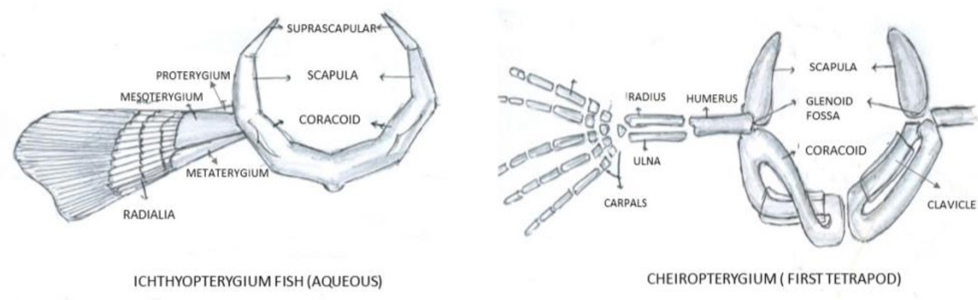


Fig 4. Diagram illustrating scheme of pectoral appendages of lower vertebrate (Aqueous) and higher vertebrate (Tetrapods).

Why five fingers per hand?

All modern tetrapods (four legged creatures), all but few fossil tetrapods, have limbs characterized by five or fewer digits. This has been viewed as an evolutionary enigma. Individuals of many species, including mice, chickens, dogs, cats and humans carry mutations which give rise to extra digits. There are examples ranging from frogs to panda bears where an additional 'finger' has evolved (Fig 5). The new 'finger' is never a true digit, however, rather in each case it is a modification of bones of the wrist, such as Panda has 6th digit which is actually an enlargement of sesamoid bone of wrist which acts as a post there by help in holding branches while eating.

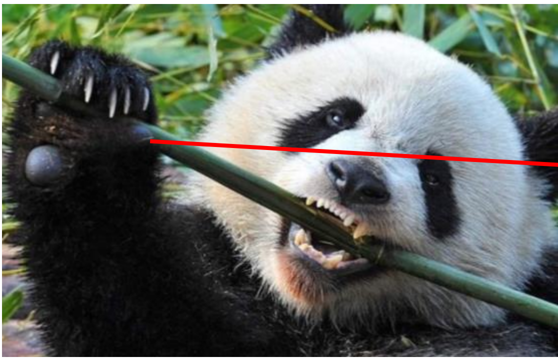


Fig 5. Panda image showing pseudo digit an enlargement of sesamoid bone helping in holding branches

This determination of pentadactyly limb is regulated by set of Homeobox genes [5]. In vertebrates, these ancestral homeobox gene cluster duplicated to give four homologous clusters. These are called Hox-1, Hox-2, Hox-3 and Hox-4. The members of all four clusters are expressed in anterior-to-posterior domains in both the embryonic central nervous system and body mesenchyme.

In the developing limb, the expression of the Hox genes of the various clusters divide the limb bud into regions along different axes. For example, the Hox-1 genes are expressed in differential domains along the proximal/distal axis, and Hox-4 genes are expressed in posterior-anterior axis. These Hox-4 genes include set of 5 (Hox- 4.4, 4.5, 4.6, 4.7, 4.8) which were expressed serially from posterior to anterior and divide into 5 zones which determine the 5 digits.Each of the five zones of the limb field can thus be considered to have a unique Hox code, or 'address' which gives the unique identity to digits. So every tetrapod is having only unique five digits.

Polydactyly is commonly seen anomaly which can be result in mutation of these Hox genes. The extra digit which is seen in polydactyly is not actually a new digit but this was genetically identical to the adjacent digit which result in expression of the mutation of Hox-4 gene.

<u>Development of specialised hand</u>

The specialised hand development started about60 million years ago with the evolution of opposable thumb. During the evolution as terrestrial animals there occurred competition for food, in order to survive the terrestrial animals started to climb trees for food and become arboreal habitat. So in due course, the size of the animals decreased and they developed prehensility of hand in order to climb trees and grab food at tree tops and edge of the branches. The further stimulus for the precision grip was the need to reach the very tip of the branch where lied the best fruit of all the trees! Simultaneously there were changes in the intrinsic muscle of hand which progressively decreased by fusion of some and disappearance of other resulting in 19 muscles in humans.The cladogram shown depicts the serial evolution of primates (fig 6).

The tarsus is the first true arboreal animal which developed first opposable thumb.

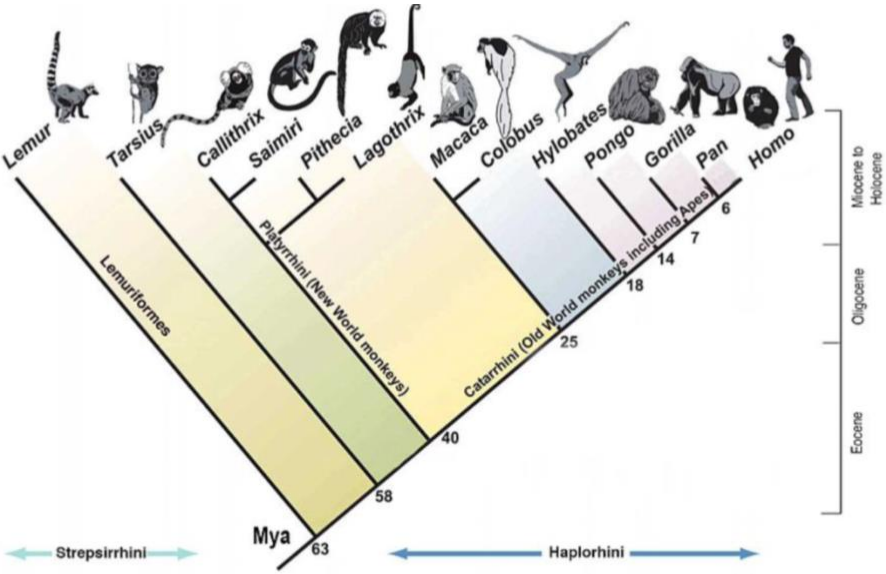
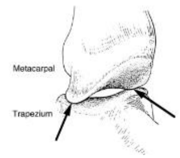
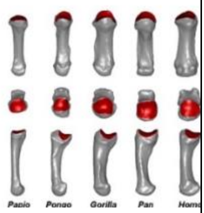
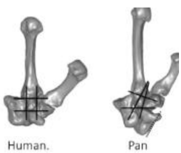


Fig 6. Cladogram depicting the evolution of primates in relation to years.

Species	Name	Evolved (Million years)
Hylobites	Gibbons	18
Pongo	Orangutan	14
Gorilla	Gorilla	7
Pan	Chimpanzee	6
Homo	Humans	1.5

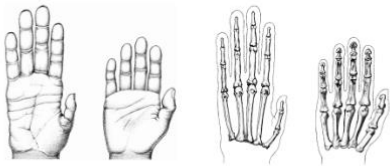
The major changes happened during the evolution were described by Napier and Marzke [1]. Based upon the fossil studies from Olduvai described by Napier in 1962, Markze described the major differences between the humans and other primates (Pan-Homo last common ancestor) based on the tool making and their usage ability [6]. Molecular evidence indicates that the last common ancestor of the genus Pan and the hominin clade existed between 8 and 4 million years ago (Ma). The current fossil record indicates the Pan-Homo last common ancestor existed at least 5 Ma and most likely between 6 and 7 Ma.The closest ancestor of species Homo was Australopithecus which had shorter fingers relative to the thumb and proximo-distally oriented articulate surface at 2^{nd} CMC joint (refer table); it existed around 2.5 Ma. So, the human hand hadevolved around 1.5 Ma.The major differences between the human hand and the hand of other primates and their significance is summarised in the table.

Table Describing the major differences in humans and other primates in respect to hand [1,2,6].

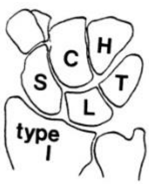
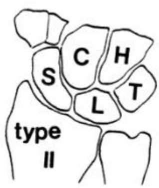
PROPERTIES	HUMAN HAND	NON HUMAN PRIMATE HAND	REMARKS
CARPO METACARPAL JOINTS 1. 1st CMC joint	Saddle joint with greater reciprocal curvature of trapezium and metacarpal surface. 	Flat joint in early primates. . But Gorilla, Chimpanzee show marked reciprocal curvature than humans. 	The curvature of human 1st metacarpal and trapezium were lie in between the flat joint and marked curvature seen in Gorilla there by increasing mobility and compromising stability. This marked reciprocal curvature seen in Gorilla provide good stability with restricted mobility and flat joint seen in early primates lack stability. Mutually curved surfaces have advantage of stabilizing joint against subluxation resulting on stable precision grip, by locking of anterior beak (along with anterior oblique ligament) against convex surface of trapezium. This result in increased stress area at that point so human 1st CMC is more prone for degenerative arthritis.
2. 2nd CMC joint	Complex of 3 articular surfaces between 2nd metacarpal base and 3 carpal	Oriented more radio ulnarly. 	Results in more parallel orientation of 2nd CMC joint to trapezoid-scaphoid joint, pronation of metacarpal and distribution of forces to capitate thereby decreasing the force on 1st CMC.

	bones, trapezium, trapezoid and capitate. Oriented more proximo-distally		
3. 3rd CMC joint	Long styloid process of 3rd metacarpal base lies dorsal to the capitate and is accommodated by distinctive bevelling of dorso-radial corner of capitate	Projection directed anteriorly and proximally into a cup on the distal dorsal radial aspect of capitate.	This styloid process along with pisso-3rd metacarpal ligament stabilizes the metacarpal against the dorsal directed forces i.e; usage of hammer stones. In nonhuman primates this process form interlocking mechanism along with other irregularities at CMC joints there preventing slide of metacarpal over capitate as body weight is borne by dorsal surface of middle phalanges during knuckle walking locomotion.
4. 5th CMC joint	Saddle joint between 5th metacarpal and hamate		Contributes 5th finger rotation towards index and thumb helping in cupping activity of hand
METACARPALS 1. Length	Shorter than apes	Longer	Along with phalangeal length results in progressive shortening of fingers and lengthening of thumb there by resulting in opposable action and better manipulation of tools.

2. Metacarpo phalangeal joints	Marked asymmetry of 2nd and 5th metacarpal heads, in which protrusion of articular surface on outer margins causes index finger to rotate towards 5th finger with flexion and abduction and reciprocal rotation of 5th finger	The orientation of articular surface is such that they will result in flexion of fingers in plane of palm without rotation.	This results in cupped position of hand along with opposable thumb. 
3. Distal palmar crease	Curved because of different level of MCP joints.	Straight because all MCP joints are at same level	This different level of MCP joints help in cupping position on finger flexion.
4. First metacarpal	Robusticity is the feature with relatively large metacarpal head breadth as compared to length of metacarpal	Gracile (slender built) Chimpanzees and baboons have relatively small head breadth	Attributed to large muscular forces across MCP joint in humans because of opposability and secure grip to hold tools

FINGERS	Relatively short compared to length of thumb	Long relative to length of thumb Narrow tuft	Opposability of fingers is possible because of shortened fingers and lengthened thumb
1. DPX	Broader apical tuft to support broad distal finger pads, Proportionately broader bases relative to tuft breadth	Base width relative to tuft width was small.	Provides support to volar pulp there by providing good precision grip 
2. Volar pads (Ungual pulp)	Functionally differentiated and compartmentalized which are stabilized distally and flexible proximally. This proximal part tethered to DPX tuft with lateral ligaments which leave marks (spines) on tufts.	Not compartmentalized These lateral ligaments are absent	Accommodate varying deformation forces from the shape of objects held by our cup like grips.

3. DPX of Thumb	Well distinct site for FPL insertion	Barely distinct site for FPL insertion area absent.	FPL was phylogenetically newer muscle which was only present in humans providing powerful precision grip there by holding and manipulating tools.
4. Proximal phalanges	Shafts are gracile with weak flexor sheaths	Robust with marked flexor sheaths	
5. Length	Shortened phalanges	Relatively longer in length.	} Curved and larger phalanges provide clinch grip in apes that help them in arboreal climbing and hanging from tree branches
6. Curvature	Straight	Curved dorso-palmarly in nature	
WRIST			
1. Trapezium	Has larger CMC joint surface and larger STT joint and more supinated in position	In non-human primates, the trapezium is positioned more in front of the trapezoid generating a deeper carpal arch.	This supinated position of trapezium alter the biomechanics of muscles reversed functionally such that the flexor pollicis brevis, opponens pollicis abduct rather than adduct and extensor pollicis adduct rather than abduct. This pronated position in nonhuman primates result in keeping the thumb in plane opposite to fingers.
2. Trapezoid	Boot shaped with expanded palmar aspect	Wedge shaped	} This palmar expansion of trapezoid causes supinated position of trapezium. This results capitate-trapezoid articulation more palmarly placed there by forces acting on 1st metacarpal are

			effectively transferred to capitate thereby reducing stress on 1st CMC joint.
3. Capitate	Expanded appearance on radial side	Waisted appearance on radial side	
4. Scaphoid (Fig 8)	Single bone	Os centralis and proximal pole are separate in baboons, Orangutan, but fused in Chimpanzees.	The relative fusion of os centralia and scaphoid result in more rigidity and stability of wrist at radial side there by preventing shear stress produced during knuckle weight bearing in chimpanzees.
5. Pissiform	Short more of pea-shaped.	Long rod-shaped.	In apes it articulate with ulna with true meniscus and helps in weight bearing.
6. Lunate	35% with Type 1 Lunate 65% with Type 2 Lunate  	Type 2 lunate  	Type 2 – the hamate form blunt facet corresponding to facet in lunate there by creating a jog in midcarpal region, which was consistent with the demands of locomotor behaviour seen in old monkeys and African humans. This pattern is prone for midcarpal arthritis. Type 1 – seen in 35% humans especially Asians in which hamate including capitate form continuous curved surface for radioulnar deviation on lunate and

			triquetrum, without creating jog. This pattern is compatible with repeated radioulnar movement increasing wrist mobility.
7. Radio carpal joint	Arc shaped radio ulnar	V-shaped wrist with deep notching of the carpus	V shaped wrist seen in apes is consistent with weight bearing activity. This increases the range of movement at wrist and combined with rotation afforded at gleno-humeral joint, provides a sphere of motion unique to humans.
8. Ulna	There was progressive shortening of ulna with formation of true meniscus	Ulna was longer and articulates with pissiform and triquetrum with true meniscus.	
MUSCLES			
1. Flexor pollicis longus	Distinct muscle belly with strong tendinous insertion into DPX.	Absent or may present with no separate belly arising from FDP tendon of index or middle finger. Extend upto DPX or terminate at PPX distally forming ligamentous slip. This prevent only hyperextension of IP joint of thumb.	In humans it is a separate belly and control IP joint of thumb and providing power in precision grip. In Orangutans FPL tendon was seen but it was arising from oblique head of adductor pollicis rather than from extrinsic mass. In baboons it arises from bifurcation of FDP tendon of middle finger.

2. Forearm flexor mass relative to forearm extensor mass	Flexors = extensors more balanced in size	Flexors > extensors	Flexors are more powerful in apes which provide powerful grip in fingers helping arboreal activity.
3. Abductor pollicis longus	Insert almost exclusively into base of 1st metacarpal	Insert strongly into base of trapezium, trapezoid, scaphoid and variably in to base of 1st metacarpal.	In apes it causes flexion but in humans it causes extension because of supinated position of trapezium.
4. Dorsal interossei	4 in number developed from the fusion of intermetacarpals, flexor brevis profundi and contrahentes digitorum.	4 in number but there was no contribution from flexor brevis profundi, they were correspond to intermetacarpals of nonmammalian tetrapods with some contribution from contrahentes digitorum.	In various mammals, including modern humans, the other contrahentes digitorum are aponeuroticor absent as independent structures. Interestingly, early in their ontogeny, modern humans have four contrahentes digitorum; that of digit I gives rise to the well-developed adductor pollicis, with perhaps some contribution from that of digit II; those of digits IV and V, as well as part of that of digit II, apparently become incorporated into the dorsal interossei. Small remnant as aponeurotic band still present in Chimpanzees at IV and V digits.
5. First dorsal interossei	Arises from approximately	Restricted to more proximo-medial	This configuration in humans provide longer lever arm for adduction of thumb than seen

	half of the metacarpal length resulting marked rugosity on the shaft	aspect of 1st metacarpal.	in great apes, and may be an important factor in various grips employed during human tool use.

Clinical significance and application of evolutionary concepts[4]

Evolution tends to favour simplicity, eliminating or fusing unwanted parts. According to the concept of Ernst Haeckel ontogeny recapitulates phylogeny the congenital anomalies can be correlated to evolutional trends. According to Lewis, early amphibians had 6 or 7 digits of upper limb providing a template for polydactyly. The pentadactyly hand became the preferred configuration 180 million years ago.

Evolutionary wise hand was classified in to foot hand (weight bearing hand) and true hand.

Weight bearing hand (foothand)

In most of non-human primates, like Gibbon, Gorilla, having a foot handi.e., the fore limbs are used while walking to bear weightso called knuckle walking locomotion and also some prehensile activity. In these the fore limbs can be used both for feeding activity and weight bearing. In these the fingers are proportionately longer than metacarpals compared to humans which are useful in weight bearing and swinging activity. There were also significant differences in the wrist like ulna is longer articulating with pisiform and triquetrum, with a true meniscus acting as a gasket between the articulation, V- shaped wrist with deep notch, ulna impaction, type 2 lunate are seen. Changes in the carpometacarpal region were also noted.In Madelung deformity there is a v-shaped wrist with deep notching of carpus as seen in foot hand of a monkey.The similar picture can be depicted during the human embryo resembling that of a tetrapod hand(fig 7). Marzke noted and illustratedthatthe projection on the 3rdmetacarpal is directed anteriorly and proximally into a cup on the distal dorsal radial aspect of capitate, there by forming interlocking feature stabilises the metacarpal against sliding on the capitateas the body weight is borne by the dorsal surface of middle phalanges during weight bearing.

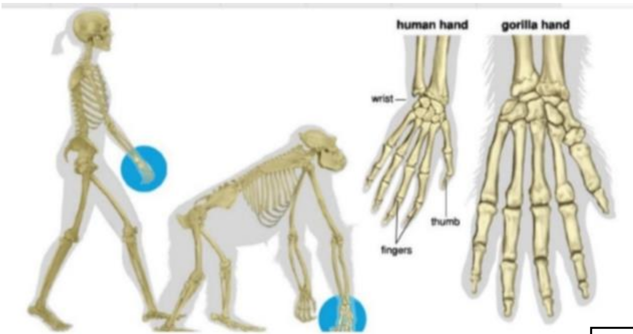


Fig 7. Depicting the difference of foot hand and true hand.

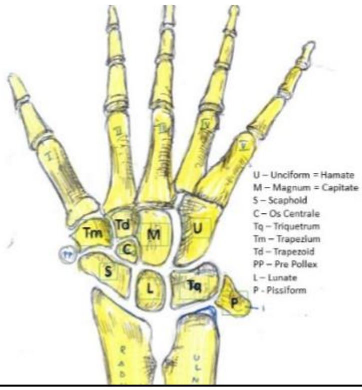


Fig 8. Hypothesized carpal morphology of an ancestral mammal, the similar morphology seen in human embryonic hand, Redrawn from Lewis (1989).

As the trunk afforded upright posture, the ulna receded along with true meniscus allowing increasing the range of movement at wrist, combined with rotation afforded with Gleno-humeral joint, this provides a sphere of motion unique to humans.

By this we can explain the deformity pattern in Madelung deformity, positive ulnar impaction syndrome (fig 9).

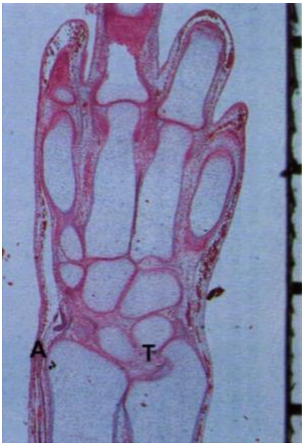


Fig 9. At 8.5 weeks of gestation, the human wrist showing similarity to a Madelung deformity and phylogenetic similarities to our ancestors compared to fig 8.

Polydactyly

As described above, early amphibian demonstrates extra digits. The genetic marker in this analogy, presumable signal events that recall the tetrapod template of wrist and hand. (Fig 9). It can be either preaxial or postaxial. It can present as simple nubbins to complex variety of nubbin. The extra digit was genetically identical to nearby digit as explained by Hox genes mutations.

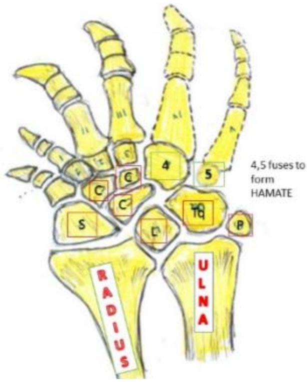


Fig 10. Early amphibian template, with polydactyly and relative radial-ulnar symmetry. Redrawn from Lewis 1989.

Syndactyly

Webbed finger related to primordial fish fins. The differentiation into digits process through apoptosis as the embryo become foetus. Incomplete differentiation causes simple or complex forms with variety of signalling abnormalities having been identified, like FGFR2 in Aperts syndrome.

Thumb hypoplasia

All great apes other than humans exhibit what resembles the various forms of thumb hypoplasia. Long fingers with relatively short thumb provides the chimpanzee with a thumb more useful as a post than for prehension, effectively as Blauth type 2 reduction (fig 11).

Fig 11. Radiograph of Chimpanzee hand showing hypoplastic thumb.

Camptodactyly

Can be explained by retained vestiges of contrahentes digitorum muscle (described in table) which was lost in evolution. These are ulnar nerve innervated intrinsic muscle thought to provide better grasp and branch negotiation for most monkeys but absent in great apes and humans. Their frequency and attachment varies in primates but usually they connect metacarpal to phalanges which help in effective graspin monkeys. Persistence of this muscle found in some humans may result flexion deformity of the fingers as in camptodactyly. Anomalous lumbrical insertion can also explained by their presence in primates.

Ulnar dimelia

The tetrapod templates of hand and forearm has more symmetry than the current template of radius and ulna orientation as governed by zone of polarizing activity. Ulnar dimelia (mirror hand) and central deficiency resemble these early tetrapod patterns; example Koala still retain this homolgy. (Fig 12)

Fig 12. Koala picture showing central deficiency

Evolution Accelerated—the Role of the Surgeon

The role of a hand surgeon in congenital anomalies is like double edge of a sword. He can advance the evolution with the stroke of the scalpel like in pollicisation of an index finger in the case of absent or severe thumb hypoplasia, or he can worsen the functional adaptation inherent in the anomaly like closure of central cleft in central deficiencies may worsen the function as child already adopts to it as like seen in koala.The majority of surgical procedures described for deficiencies and duplications, including reduction and construction of duplicated digits, syndactyly release, tendon transfers and repositioning of the hypoplastic thumb, and ulnar levelling procedures for Madelung deformity, improve both the function and appearance of the hand. While considering the surgical indication one has to perfectly balance the aims of improving the function and achieving the shape of the hand.

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