
ORIGINAL COMMUNICATIONS

Presidential address: The hand and evolution

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A few years ago my predecessor and colleague, James H. Dobyns,¹ played the part of a futurist and speculated on the progress of our specialty in the next 25 years. For several reasons, I thought it would be interesting to reverse our perspective and consider the tortuously long evolutionary history of the upper extremity.

Founded 45 years ago under the guiding influence of Sterling Bunnell, the American Society for Surgery of the Hand has evolved from an elitist club in which membership was a coveted privilege into the largest forum available to promulgate, assess, and stimulate progress in the medical and surgical treatment of hand problems.

The evolution of the hand was a favorite subject of Sterling Bunnell, and the first chapter of his book, *Surgery of the Hand*,² is entitled "Phylogeny and Comparative Anatomy." This is a detailed description of the

evolutionary development of the upper limb, written by an enthusiast who was well versed in the contemporary literature.

The hand in evolution can be interpreted from a metaphorical perspective as well. Certainly our first meeting in Canada brings to mind the *hand of man* as exemplified by the acid rain problem and leads us to consider the ramifications of human activity on the biologic evolution of this planet.

Finally, the selection of an evolutionary theme has to do with the feeling of awe that most of us have for the hand. We all share a fascination with the anatomy and function of so versatile a part. This wondrous tool hanging at the end of our arms and the complicity of nature to allow exploitation of its potential are paramount to the perilous transition we have made through time. A lithograph by M.C. Escher captures the essence of the importance of the hand in the context of man's place in the universe. The reflection in the globe reflects the disparity of motor and sensory representation in the cerebral cortex; the library setting, the relationship of intelligence to the adaptive hand; and the reflected visage of the artist, the contemplation of the unique properties with which his hand is endowed (Fig. 1).

This preoccupation with the advantage the hand provides is age-old. Aristotle³ noted:

In man the forelegs and forefeet are replaced by arms and by what we call hands. For of all animals man alone stands erect, in accordance with godlike nature and essence. For it is the function of the godlike to think and to be wise; and no easy task were this under the burden of a heavy body, pressing down from above and obstructing by its weight the motions

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Fig. 1. Lithograph of Escher on the globe (described in text). (From Locher JL, ed. *The world of M.C. Escher*. New York: Harry N. Abrams, Publishers, 1971. ©1935 M.C. Escher/Cordon Art, Baarn, Holland. By permission.)

of the intellect. . . . Standing thus erect, man has no need of legs in front, and in their stead has been endowed by nature with arms and hands. . . . This instrument . . . has been given by nature to man, the animal of all animals the most capable of acquiring the most varied handicrafts.

To be “in the hands of God,” to be brushed by the hands of God, and “to sit at the hand of God” all signify the anthropomorphic association with which human beings have portrayed their religious feelings. It is not difficult to understand our literal interpretation of creation through divine hands. Human experience suggested that all useful modifications to material objects were performed by hand. The gift of hands that allowed man virtually alone, among all life on earth, to prepare food, nurture fire, and create tools could seemingly derive only from a deity of similar form. Sir Charles Bell,⁴ in his contributions to the *Bridgewater Treatises*, entitled his work on the anatomy of the hand

as a scientific proof of the existence of God *The Hand: Its Mechanism and Vital Endowments as Evincing Design*. He captured the essence of such mythic feeling when he said: “We have seen that the system of bones, muscles, and nerves of this extremity is suited to every form and function of vertebrated animals; and we must confess that it is in the human hand that we have the consummation of all perfection as an instrument.”

Charles Darwin⁵ brought that comfortable association of man and creator to a jolting reassessment. In the 134 years since the publication of *On the Origin of Species*, the explosion of anthropology, embryology, paleontology, and geology has been incredible; much of it, indeed, has occurred within our lifetimes.

In his recent book, *Wonderful Life: The Burgess Shale and Nature of History*, Stephen J. Gould⁶ suggested that human development is an unlikely accident and that any replay of natural history with the slightest alteration in the sequences of natural selection would in all likelihood not only squelch the development of man but, for that matter, any species with the possibility of attaining abstract intelligence. The “slow and slight progressive modifications” of natural selection based on adaptive characteristics suggested by Darwin has been modified by Gould⁷ and others⁸ to a more chaotic theory of “punctuated equilibrium.”

Gould⁶ suggested that, rather than a single stem of life slowly proliferating into a great diversity of life forms over time, an initial period of great diversity occurred with a burst of multicellular animals 500 million years ago in the Precambrian period. These have since undergone periodic decimations associated with catastrophic events that punctuate geologic time into eras, periods, and epochs. In the equilibrium phases, speciation—a disparity based on similar body plans, rather than a diversity of plans—developed to fill the ecologic niches. It is worth noting that the impetus for the changing views on evolution is based in part on the findings from a remarkably preserved fossil field in the Province of British Columbia in our host country, Canada. This small area, known as the Burgess Shale, holds an amazingly rich preservation of soft-bodied fauna that provides a window in time to the early Cambrian period.

I would like to trace the development of the hand from an amateur’s perspective. The literature is far too detailed and extensive for me to try more than to describe some generalities, but I hope you will share my enthusiasm.

Evolution of life on earth

It is generally accepted that life developed photochemically in a reducing atmosphere 1 billion years

after the earth's formation.⁹ Nucleic acids and proteins in cellular form gave rise to the first life of which we have evidence, prokaryotes. These are similar to the bacteria and algae of today and lived as symbiotic mats, preserved as stromatolites that date back 3.5 billion years. Derived from amalgamation and endocellular symbiosis are eukaryotes, larger nucleated cells that have recently been shown to exist through an almost equivalent period.¹⁰

Some 560 million years ago an oxidizing atmosphere on which multicellularity is dependent developed. The mitochondrion, another intracellular symbiont, allowed the much more efficient oxidative respiratory system to develop.

The culmination of such modifications resulted in an explosion of multicellular organisms known as the Ediacaran proliferation at the beginning of the Cambrian period.¹⁰ This produced not only all the current phyla—with the possible exception of the Chordata, from which the vertebrates were to evolve—but also a plethora of other life forms.

The earliest suggestion of a chordate is seen in an example from the Burgess Shale, which was given the name of *Pikaia gracilens*.⁶

Biomolecular control of segmentation and cephalocaudal polarity has posed, until quite recently, a marked problem in our understanding of development.^{11,12} However, the discovery of homeobox genes, which elaborate a 60-amino acid sequence known as a homeodomain, offers a solution to this problem. The function of this polypeptide link on homeodomain proteins is to recognize and bind to specific DNA sequences in such a way as to activate or to suppress the expression of subordinate genes. They are responsible for first ordering the head-tail polarity in the developing gastrula and then the subsequent development of body parts. The development of the upper extremity is regulated in a specific sequence in this way. The fascinating aspect of these genes is their apparent primitiveness. They appear to be virtually identical in invertebrates such as centipedes, worms, and insects to those in vertebrates, although the vertebrates may have benefited from diploidy.

Evolution of fish

From later Chordata, perhaps similar to modern amphioxus, there arose in the late Cambrian and Ordovician periods 440 million years ago small, finless vertebrate fish with cartilaginous skeletons, jawless mouths, and bony armor that are called ostracoderms.¹³ Alone among the Agnatha in the late Silurian and early Devonian eras arose a poorly defined group, cephalasids, which developed paired fins with an unknown

internal structure. They are thought to have pursued a benthic, or bottom feeding, existence in view of their broad, flat ventral surface. This feature may be important to the next group.

The succeeding Devonian period began 390 million years ago as plant life was beginning to infiltrate land. The development of an ozone layer diminished the necessity for the protection of aquatic existence from solar ultraviolet radiation. This period witnessed the development of jawed fish.¹⁴ The placoderms were heavily armored, and some developed both pectoral and pelvic fins.¹³ Later in the same period, the evolution of the fish that would provide the precursors for the vertebrate limbs occurred. All living fish belong to the *Chondrichthyes* with cartilaginous skeletons or *Osteichthyes* with bony skeletons. The latter may be divided into two groups: the actinopterygii (ray-finned fish) and sarcopterygii (flesh-finned fish). The former, with greater maneuverability and more efficient swimming design, were so successful that they represent virtually all fish extant today. The latter, which represent the precursors of all terrestrial vertebrates, were the dominant fish of the earlier era.^{13, 15}

The sarcopterygii may be divided into *Crossopterygii* and *Dipnoi*, or lungfish (Fig. 2). Of the former, a further division in coelacanth (hollow spine) and rhipidistians (sail fins) can be made. The latter presented an articulated bony skeleton activated by muscle within the fins. This provided the basis for limb development. Both classes were thought to be long extinct until a coelacanth was unexpectedly discovered in a pile of trash fish caught near the Comoro Islands in 1938.¹⁶ Several hundred specimens have been caught and analyzed since then, and more recently these fish have been studied in their natural environment, with underwater photographs taken at depths below 100 meters.¹⁷ They are piscivorous drift feeders that stabilize their orientation with synchronous alternation of paired fin motion that is reminiscent of primitive tetrapod locomotion. This cousin of our rhipidistian forebears provides marked insight into the physiology and anatomy of these primitive fish.⁵

The rhipidistians became extinct by the lower Permian period. They were predatory shallow freshwater bottom feeders that probably used their fins for locomotion through the mud and detritus of estuarine and tidal areas.¹⁶ Their shoulder girdles consisted of both dermal and endochondral elements. The former were a direct continuation of the opercular series and skull roof. The shoulder girdle consisted of a large ventrolateral cleithrum which supported a scapulocoracoid. Paired clavicles and an intraclavicle passed medially. The last feature of special importance was a swim blad-

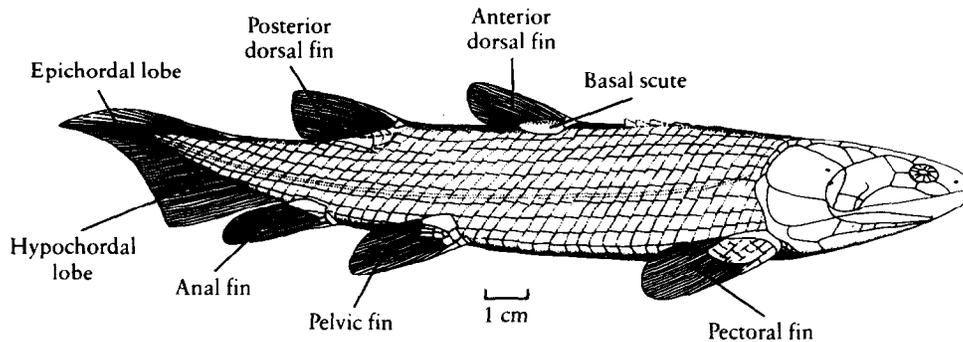


Fig. 2. Osteoleptiform rhipidistian sarcopterygian fish from the Devonian period. Bony elements within the pectoral, pelvic, anal, and posterior dorsal fin are controlled by integral muscles. (From Moy-Thomas JA. *Palaeozoic fishes*. 2nd ed, revised by Miles RS. Philadelphia: WB Saunders, 1971. By permission of Chapman and Hall.)

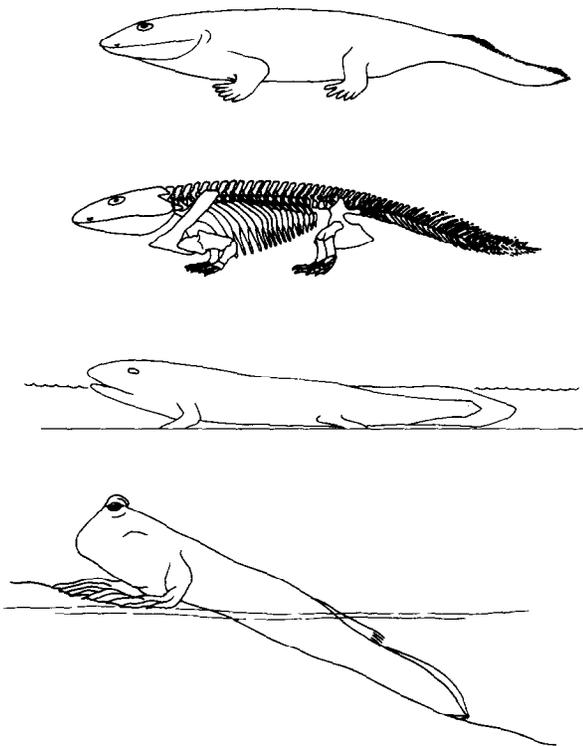


Fig. 3. The pectoral fin in shallow waters was instrumental in holding the head out of water for respiration. Forward flexure at the elbow developed on that basis. (Excerpted from Thomson KS. *The living fossil: the story of the coelacanth*. Copyright ©1991 by Keith S. Thomson. Reprinted with permission of the publisher, W. W. Norton & Company.)

der that originally served as a device to alter buoyancy but may have allowed these fish to spend increasing periods out of water, similar to their surviving cousins, the modern lungfish.¹⁵ The rhipidistian differed from

the modern coelacanth, which has a fat-filled swim bladder. Shallow warm waters with decaying vegetable matter would have a low oxygen concentration, forcing increased reliance on air breathing. The pectoral fins thus became supportive in holding the head out of water for breathing, while the hind limbs helped to move the body in the mud of the shallow pools (Fig. 3). The forward flexure of the elbow, which persists in terrestrial vertebrates, appears to have developed because of the necessity to support the cephalad portion of the fish. The primitive skeletal structures of the pectoral fins are readily recognizable and will be discussed with the comparative osteology of the later amphibians, reptiles, and mammals¹⁶ (Fig. 4).

Primitive amphibians have so much in common with the rhipidistians that there is no serious quarrel as to their derivation.¹³ The alterations that adaptation to terrestrial life required were extensive. The body, no longer buoyed by water, required a stronger vertebral column, ribs, and muscles. Feeding before the development of a muscular tongue necessitated an upward tilting of the head to swallow. Respiration required depression of the hyoid followed by an elastic rebound of the thorax. An impermeable skin was necessary to prevent desiccation. Sensory input from the lateral line was no longer effective and required the development of better sense organs in the skull. Proximity to water for reproduction was essential. The energy expenditure for foraging, respiration, and reproduction increased markedly.

Terrestrial transition

Ninety-five percent of marine fauna perished in the Permian extinction, which marked the end of the Paleozoic period and the beginning of the Mesozoic period. The successful terrestrial transition is represented

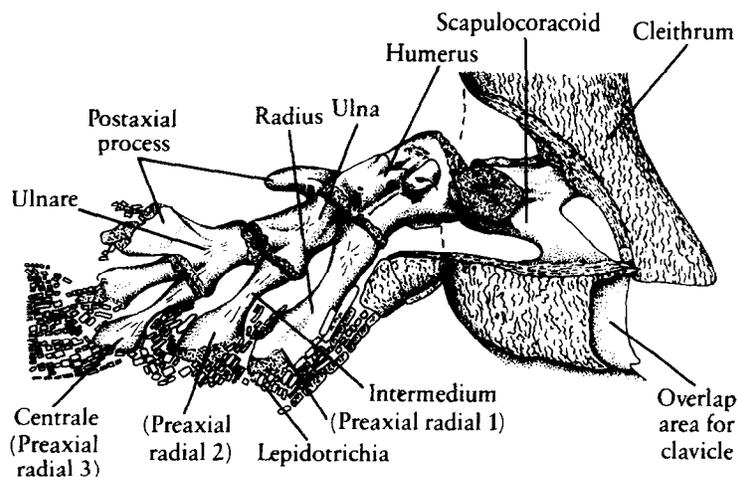


Fig. 4. The pectoral fin of the osteoleptiform shows the basic osseous structure of subsequent vertebrates. The parallel bones distal to the humerus allow development of the forearm. The modern coelacanth *Latimeria* has only a single bone in a comparable position. (Modified from Andrews SM, Westoll TS. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans R Soc Edinburgh* 1970;68:207-329.)

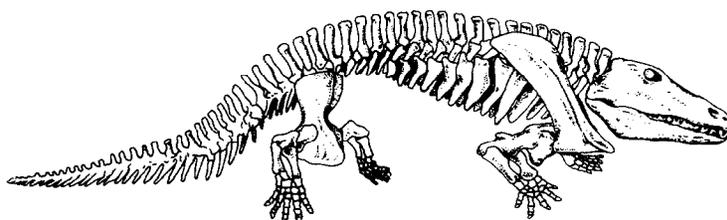


Fig. 5. *Eryops megacephalus*, early Permian amphibian, approximately 2 meters in length. (From Gregory WK. *Evolution emerging: a survey of changing patterns from primeval life to man*. Vol. 2. New York: The Macmillan Company, 1951. By permission of the American Museum of Natural History.)

by *Eryops*, an amphibian 3 meters long (Fig. 5). Enhanced pelvic and pectoral girdles were developed to transfer weight from body to limbs, but their lateral position required considerable muscular effort for locomotion. Despite the limitations of the relatively inefficient limbs, amphibians were the dominant land animals from the close of the Devonian period 370 million years ago until the oxygen-permeable and desiccation-resistant egg gave the reptiles *the upper hand* 70 million years later.¹³

The later Mesozoic era, the age of reptiles, lasted from 225 to 65 million years ago and ended with the extinction, during the Cretaceous period, of the dinosaurs and most species of reptiles. During that long period they were amazingly successful in elaborating environmental adaptations. The early representatives of this group were small lizardlike insectivores with a

more fully ossified skeleton and most likely increased agility attributable to muscle stretch receptors. Reptiles are divided into three classes on the basis of temporal fenestrations: anapsids (turtles), diapsids (dinosaurs), and synapsids, which represent the basis for mammalian evolution. From therapsids, recognizable by the upper Permian period, the earliest direct mammalian predecessors—the cynodonts—appeared. These small nocturnal animals subsisted in the shadow of the dominant dinosaurs but had already developed an oxidative metabolism in contrast to the fermentative one of the other reptiles (Fig. 6). They required an order of magnitude more oxygen and food per body weight.¹³

At the end of the Mesozoic era and the beginning of the Cenozoic era, the earth was again visited by the *heavy hand* of mass extinction. Known geologically as the K-T interval, this event is marked by a thin layer

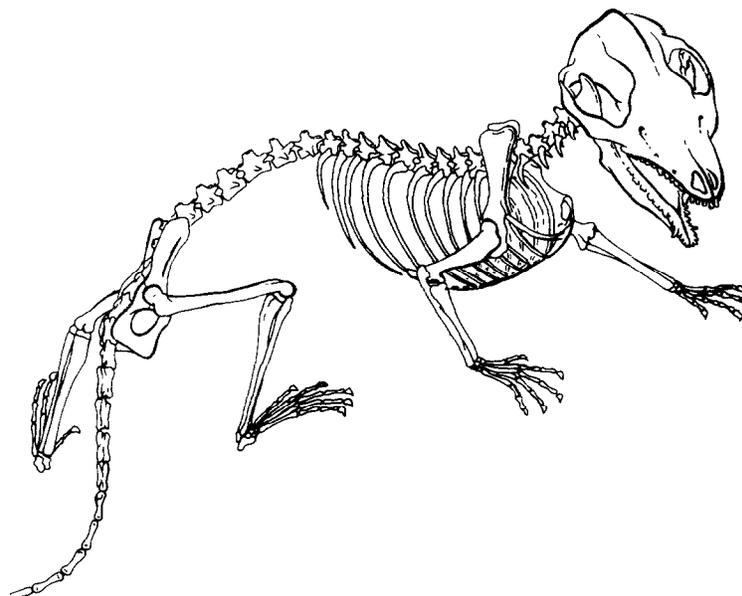


Fig. 6. Morganucodon, early Therian mammal, late Triassic and early Jurassic age, approximately 10 cm in length, nocturnal insectivore, weight 20 to 30 gm, mammalian vertebral pattern, carpal centrales reduced to two, limbs approaching the parasagittal position. (From Jenkins FA Jr, Parrington FR. The postcranial skeletons of the Triassic mammals *Eozostrodon*, *Megazostrodon* and *Erythrotherium*. *Philos Trans R Soc Lond [Biol]* 1976;273:387-431. By permission of The Royal Society.)

of iridium-rich sediment that occurs in a worldwide distribution. The theory of climatic upheaval, catastrophic to dinosaurs as well as to other large segments of the flora and fauna, is now undisputed, and some have forwarded a persuasive argument for a period of unusual volcanic activity.^{18, 19} However, because iridium is known to occur in greater concentrations in meteors, Alvarez and Asaro²⁰ postulated that an immense meteor strike was sufficient to induce a profound and lasting climatic change.

Tektites, shocked crystals, and fossil leaf patterns seem to favor the impact theory.¹⁸ That this event allowed the emergence of mammalian ascendancy seems incontrovertible, and, as we shall see, further geologic and climatic change was crucial in primate evolution.¹³

Evolution of the forelimb

Skeletal development. The humerus, radius, and ulna are recognizable in the fossil rhipidistian pectoral fin. The humerus articulates with the scapulocoracoid proximally and with a long bladelike radius and shorter ulna distally. The ulna articulates with an anterior, an intermedium, and a posterior ulnare, which in turn are extended by two additional bones representative of later additional carpals. Distal to this, small bodies named lepidotrichia give additional support to the fin¹³ (Fig. 4). It is likely that the forward flexion at the humero-

ulnar articulation had already taken place as an adaptation to bottom feeding and air breathing.

The most primitive amphibians have five rays and 11 or 12 carpal bones arranged in a blocklike mosaic pattern of three rows (Fig. 7). In early amphibians there may have been up to seven digits, but in most later and all modern amphibians there is a four-digit configuration with a phalangeal sequence of 2, 2, 3, 2.^{21, 22} The limbs are directed laterally from the body. The mechanical disadvantage required short sturdy bones with prominent muscular attachments. The joints allowed for limited motion.

The basic morphology in reptiles becomes more recognizable. The carpal bones are reduced to 10, of which 5 are the distal carpals supporting the metacarpals in a pentadactylate plan. Whether the reduction in the number of carpal bones occurs by coalescence or elimination is not known.²¹ The phalangeal sequence is 2, 3, 4, 5, 3. The limbs move further under the body, providing more support and greater speed and agility. The bones are longer. Some of the sphenodontid lizards developed physes whose closure limited growth and provided for better joint formation, as in the later mammals.¹³

Osseous morphology in mammals varies widely among the families, but that in primates closely follows the primitive reptilian plan except that the phalangeal

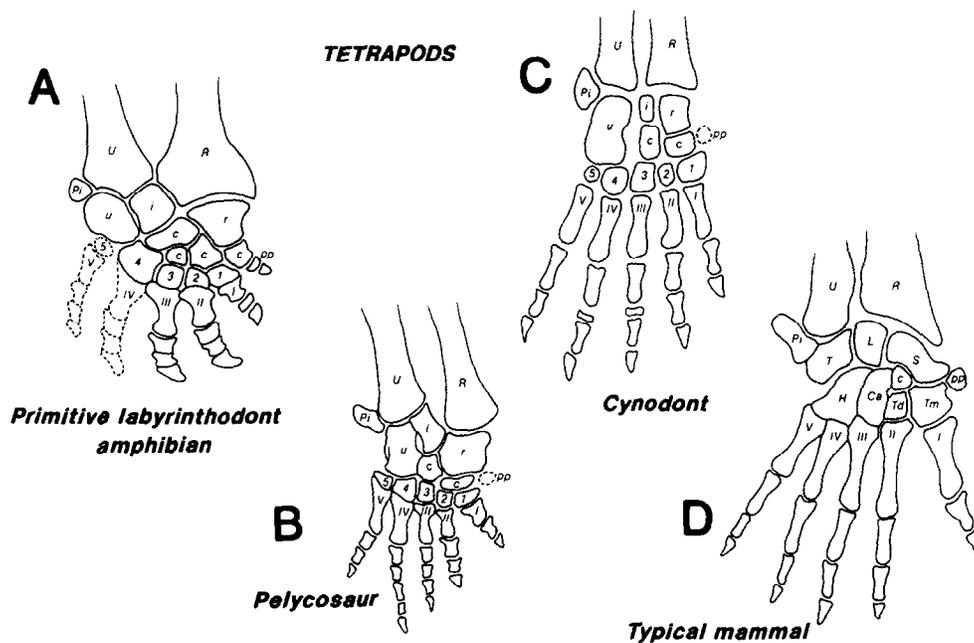


Fig. 7. Inferred transformation of the carpal architecture of the tetrapods based on descriptions and interpretations by various authors. **A**, Primitive labyrinthodont amphibian; **B**, early mammal-like reptile pelycosaur; **C**, advanced mammal-like reptile cynodont; and **D**, typical mammal. (From Lewis OJ. *Functional morphology of the evolving hand and foot*. Oxford: Clarendon Press, 1989. By permission of Oxford University Press.)

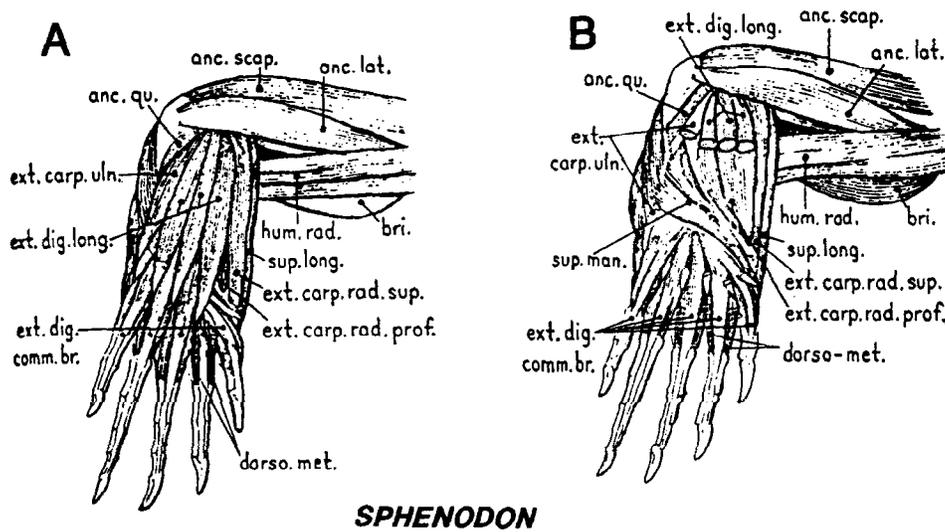
sequence became 2, 3, 3, 3, 3, probably by elimination of disklike intermediate segments.²¹

Muscular development. The evolution of the musculature of the upper extremity from amphibians through the reptiles provides a fascinating progression of increasing differentiation and mechanical efficiency.²¹⁻²³ Because the limbs are lengthened and displaced medially, mechanical efficiency is improved. At the same time, displacement of muscle mass also moves the mass moment of inertia proximally, allowing for faster limb acceleration.

In the reptile the extensor musculature shows increasing differentiation to individual digits. The extensor digitorum communis brevis appears to provide precursors to the proprius muscles of human beings (Fig. 8). The conjoined palmar aponeurosis of the palmaris communis superficialis and profundus splits into two layers. Continuity is established directly from the latter muscle (perforatus) to the terminal tendons by incorporation of the middle layer of the flexor brevis medius. The slips of the most superficial layer of the flexor brevis have migrated and twisted around either side of the terminal tendon to insert onto the basal aspect of the second-most proximal phalanx (Fig. 9). Proximally, the flexor brevis superficialis retains its attachment to the

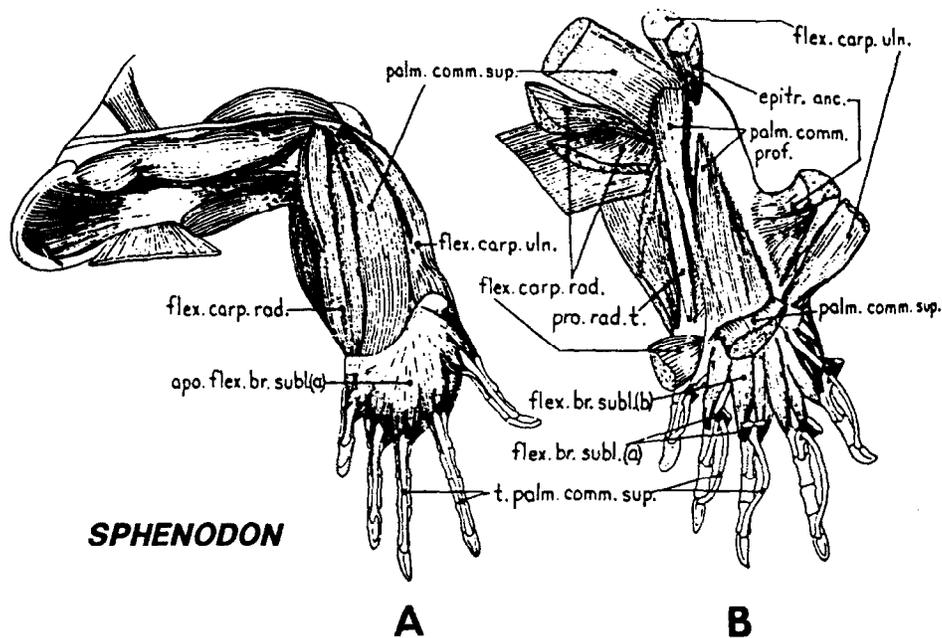
undersurface of the superficial aspect of the palmar aponeurosis. This, in turn, is attached to the pisiform and radiale. The palmar aponeurosis forms a bridge over the flexor profundus analogous to the flexor retinaculum of mammals. The distal attachment presages Camper's decussation of the flexor superficialis (perforans) in mammals. The middle layer of the flexor brevis medius is the precursor of the tendons of the flexor digiti profundus, as already noted, and also gives rise to the lumbricals. The deep stratum of the flexor brevis medius is thought to give rise to the contrahentes.²² These form four adductor muscles in amphibians and persist with greater distinction in reptiles and mammals.²³⁻²⁵ Except for the adductor pollicis, however, the other three are absent in the human upper limb. The deep flexores breves gave rise to the palmar interossei. In the primitive model there would be two—one on either side of each digit.

Continued differentiation is seen in the musculature of the marsupials and later mammals. The palmaris communis superficialis becomes the flexor superficialis communis with incorporation of the tendinous attachments of the flexor brevis superficialis. It may be worthwhile to return to this area as primate adaptations are discussed.^{21, 26, 27}



SPHENODON

Fig. 8. Dorsal musculature of sphenodon, extant primitive reptile of Tasmania. Note increased differentiation of extensor musculature and length of limb. *A*, Superficial. *B*, Deep. (From Miner RW. The pectoral limb of *Eryops* and other primitive tetrapods. Bull Am Museum Natural Hist 1925;51:145-312. By permission of the American Museum of Natural History.)



SPHENODON

A

B

Fig. 9. A, Flexor palmaris communis profundus has completed its attachment to the terminal phalanx by incorporating the superficial aspect of the flexor breves intermedius. Palmaris communis superficialis is attached to the palmar aponeurosis, which bridges the carpus. The flexor brevis superficialis have formed and are passing around the terminal tendons as precursors to the flexor superficialis of mammals. **B,** Superficial layers of muscle are reflected, exposing deep musculature. (From Miner RW. The pectoral limb of *Eryops* and other primitive tetrapods. Bull Am Museum Natural Hist 1925;51:145-312. By permission of the American Museum of Natural History.)

Primate evolution. Primitive mammalian stock characterized by more efficient limb posture, an oxidative respiratory system, separation of the cardiac ventricles, separation of the air passage by a secondary palate, and other specializations¹³ was present as early as the late Triassic period, 200 million years ago. At the end of the Cretaceous period small, nocturnal, and fecund opportunists were ready to fill the void left by the extinction of the dinosaurs and other reptiles. The morganucodon (Fig. 6), about the size of the modern squirrel, was representative of these animals. These small endothermic quadrupeds were probably arboreal insectivores that developed hair for temperature control and later had sweat and sebaceous glands. Nocturnal life in a hostile forest environment led to the development of increased sensory acuity and a correspondingly larger brain. Their legs approached and rotated into the sagittal plane, providing greater locomotor efficiency and, by statically supporting the body, improved energy conservation at rest. The spine became more mobile in the sagittal plane.¹³ The rear legs rotated the knee forward and the forelimb rotated the elbow backward so that the planes of motion of the limbs were in the plane of forward motion of the body. This arrangement allowed greater agility for escape as prey and for capture as predator. The rotation of the elbow necessitated pronation of the radius on the ulna to align the forefoot. This, in turn, has facilitated the development of the radioulnar joints and rotatory movement of the forelimb, enhancing further differentiation and development of the pronator and other forearm musculature.

Increased speed and agility require that the primary propulsive effort be provided by the hind legs. The body must be lifted off the ground against gravity, with the forelimbs acting to decelerate both forward and downward motion. This deceleration is best absorbed by muscles rather than by rigid fixation to the axial skeleton, as in the pelvic girdle. The pectoral girdle is thus increasingly suspended from the cervical and thoracic spine by circumferential muscles. The adaptation opens the way for the development of a remarkable range of shoulder motion in the later suspensory apes.

The earliest recognizable primates appeared in the early Eocene period, around 55 million years ago.^{28, 29} They were equivalent to the tree shrews, lemurs, and tarsiers of today. They acclimated to the spreading hardwood forests, where their small size, mobility, and arboreal existence provided protection and a diet of insects and small lizards. For clinging in the branches, longer and broader digits developed, and the claw thinned and moved dorsally as a nail. The eyes moved

to the front of the head, facilitating binocular vision. Integration of visual, auditory, and olfactory senses resulted in increased cranial size. These early primates flourished in the moist tropical climates of the Eocene period, but their numbers decreased drastically in the Oligocene period with sharper changes in seasonality. Anthropoidea became evident in the Oligocene period, and apes were widespread in the expansive forests of the Miocene epoch, beginning 25 million years ago.¹³

A mobile shoulder and a greater rotation of the forearm favored arm suspension and brachiation, the ability to swing progressively from hand to hand along a branch.^{30, 31} Monkeys, although amazingly agile in the arboreal environment, rely on a quadrupedal gait and have limited shoulder motion compared with the apes (Fig. 10). They have an average forearm rotation of 90 degrees compared with 160 degrees in apes and human beings.^{32, 33} Arboreal life also favored an erect posture for movement, feeding, and surveillance.

The apes, as in other areas, diverged into various ecologic niches. Increasing size and weight, as well as foraging opportunities on the forest floor, led to forays out of the trees, much as is seen in present-day chimpanzees. A semierect posture promoted knuckle walking, as seen in chimpanzees and gorillas. Neither of the apes, however, can walk well or efficiently in a bipedal stance, although their hands are freed for independent use part of the time.²⁹ Knuckle walking may be responsible for development of the deep intermetacarpal ligament in these apes as a resistance to metacarpal spreading in the compression mode. The prominence of this ligament in human beings may be based on a similar mechanism but quite a different activity.

In the late Miocene epoch, contraction of the forests and increasing expanses of savannah occurred as the Tethys Sea was closed by the impaction of the Arabian Peninsula in Asia, inducing an increasingly arid climate.^{13, 28, 34} A marked depletion of Miocene apes occurred, as they were literally and figuratively left out on a limb. Survival in the open, which became increasingly populated with efficient predators, was hazardous at best. It is most unlikely that the hand at that period was capable of wielding more than the most rudimentary of weapons; its greatest asset was still the ability to allow the animal to retreat into the branches.

The thumb. Central to the improvement of hominid hands over those of the great apes is the development of a strong and more opposable thumb. It is not only relatively larger and longer, but it can rotate to oppose all of the fingers. Aristotle³ described this well:

The joints, moreover, of the fingers are well constructed for prehension and for pressure. One of these also, and this

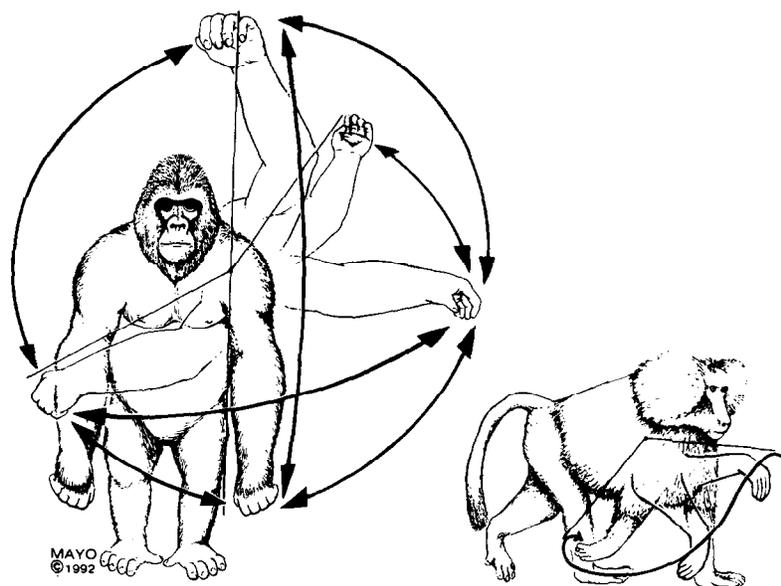


Fig. 10. The gorilla retains the hemispheric range of shoulder motion associated with suspensory life and brachiation as well as a marked pronosupinatory range. The baboon is, by contrast, a quadruped with more limited shoulder and forearm motion. (By permission of Mayo Foundation.)

not long like the rest but short and thick, is placed laterally. For were it not so placed all prehension would be as impossible, as were there no hand at all. For the pressure of this digit is applied from below upwards, while the rest act from above downwards; an arrangement which is essential, if the grasp is to be firm and hold like a tight clamp. As for the shortness of this digit, the object is to increase its strength, so that it may be able, though but one, to counterbalance its more numerous opponents (p. 687b).

Galen³⁵ recognized the functional significance of his anatomic studies when he stated: "But when [nature] placed the thumb in opposition to the other fingers, she realized that the lateral movements of the fingers in the direction of the thumb would be very advantageous."

To be sure, to use our hands freely, it is necessary to stand in an erect balanced posture. Standing erect requires a plantigrade foot, a lordotic spine, and large gluteal muscles. It has been popular to suppose that increasing brain size, development of the opposable thumb, erect posture, and a bipedal gait occurred in that order or at least simultaneously. Would our human pride be offended if a flat foot and a large buttock were antecedent to hand and brain development? This question has been answered to our dismay by the fossil finds that Dr. Johanson³⁶ showed us earlier as well by Mary Leakey's discovery of the Laetoli footprints.³⁷ These finds suggest that the early hominids such as "Lucy" walked erect at least a million years before the demonstrated use of tools.^{34, 36, 38}

Lovejoy³⁸ asserted that bipedalism was established before the permanent venture onto the savannah and that the reasons for this involved a complex interaction that has to do with reproductive survival. Many other factors have also been thought to have led to bipedalism, including foraging and protective behaviors.

From the standpoint of human time, the progression from our most probable direct apelike ancestor, dryopithecus (*Proconsul*), which was present 17 to 8 million years ago, to the present seems an eternity. *Ramapithecus* and *Sivapithecus* followed 7 million years ago and the earliest *australopithecines* 4 million years ago.²⁸ As Marzke³⁹ showed us, the latter were equipped with hands that had distinct characteristics of human and ape hands. She and others⁴⁰⁻⁴⁴ further demonstrated that the use of tools may well have had a remarkable influence on the morphologic changes that led to the present configuration of our hands. Among these changes, she cited the enlarged thumb, modification of the first metacarpotrapezoidal joint, enlargement of the second metacarpotrapezotrapezoidal joint, enlargement of the third metacarpal styloid, alterations at the metacarpohamate area, and decreased length of the pisiform. The last, along with the decreased length of the ulna and ulnar styloid, improves ulnar deviation.⁴⁴

The ape grip, designed primarily for hanging, is aided by long curved digits with very strong osseous ridges to support the annular bands of the flexor sheaths, which must support the animal's weight⁴⁵ (Fig. 11).

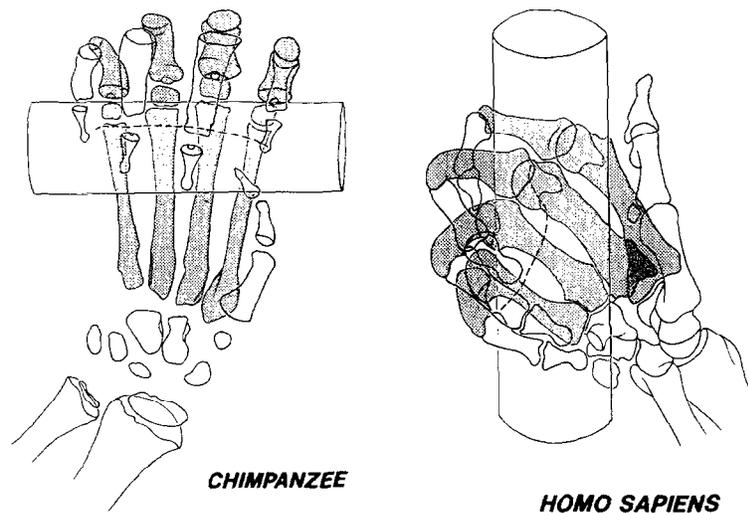


Fig. 11. A, The right hand of a 2-year-old chimpanzee with a power grip drawn from an x-ray film. B, The right hand of a human being in a precision grip that allows a grasped object to be aligned with the longitudinal axis of the forearm. (From Lewis OJ. *Functional morphology of the evolving hand and foot*. Oxford: Clarendon Press, 1989. By permission of Oxford University Press.)

Wrist extension and ulnar deviation in the chimpanzee are limited in comparison to human beings.⁴⁶ Use of sticks or other objects for tools is restricted by the inability to align them with the long axis of the forearm. Tool use and stone tool formation are markedly aided by a grip that allows the object to be encompassed and manipulated through multiple small movements.⁴⁷ The opposable thumb obviously is key to this ability, but increased mobility of the fourth and fifth metacarpals provides the counterpressure from the ulnar aspect of the hand. The increased ulnar deviation permits hammering as well as linear alignment of tools with the forearm. Marzke and Shackley⁴¹ showed that formation of stone tools uses this type of gripping. The pronation of the second metacarpotrapezoid joint with the additional support from the added trapezial facet helps to resist or dampen the stresses associated with resisting the pollical forces perpendicular to the finger flexion plane. The larger third metacarpal styloid resists the shock of impact to ballistic forces on the hand. The proximal angulation of the hamulus and the increased ligamentous attachment areas on the palmar aspect of the hamate allow for improvement of the adaptive grasp of human beings.⁴⁸

Other changes that improve grasp are the increased width of the terminal phalanges, which support a more object-adaptive pulp, dermal ridges, and their enclosed sweat glands.⁴⁹ These modifications were sufficient to allow the development of stone tool manufacture, which is associated with the 2-million-year-old fossil remains of *Homo habilis*, or "handy man," as named by Louis

Leakey.⁵⁰ *Homo erectus*, the next direct antecessor of modern man, appeared about 1.6 million years ago and became so successful that his remains are found throughout Africa, Asia, and possibly Europe. Neanderthal and Cro-Magnon, both *Homo sapiens*, emerged prior to the last ice age, with the former perhaps succumbing to the skill and cunning of the latter despite Neanderthal's robust muscular frame.

The modern hand has some last modifications from its predecessors. The four conrahenes that provided finger adduction were reduced to one. This is the powerful adductor pollicis that is so important to the adaptive grip. The other three conrahenes may be represented by the intermetacarpal ligaments and the fascia overlying the interossei. Again, tool use may have played a large part in this modification.³⁹ Galen³⁵ first described the seven palmar interossei in the ape hand that remain from the primitive flexor breves profundi of the amphibian. These are reduced to three in man if the accessory adductor pollicis is ignored. These three palmar interossei act as adductors as well as phalangeal extensors and are positioned opposite the insertion of the dorsal interossei. The other four palmar interossei have been incorporated into the overlying dorsal interossei, but they may be distinguished by careful dissection and recognition of their greater fiber length. They retain their independent action on interphalangeal extension.²¹

We know that we share 96% of our common genes with our African ape cousins. From the assumed mutation rate, our common ancestry is some 7 to 9 million years old.⁵¹ We know that the mitochondria that power



Fig. 12. Escher has captured in this lithograph the pentadactylic evolution of the tetrapod and suggested the development of intelligence by inclusion of a book, a mythic relation of the 20 digits to the dodecahedron, and perhaps the eventual slide back to our origins. (From Locher JL, ed. *The world of M.C. Escher*. New York: Harry N Abrams, 1971. ©1943 M.C. Escher/Cordon Art, Baarn, Holland. By permission.)

our muscles and oxidative systems date from the Precambrian era and that there is a possibility that every *Homo sapiens* alive today may have inherited mitochondria from one woman within the last few hundred thousand years, according to the estimated mutational divergence rate for human mitochondrial DNA.^{52, 53}

Conclusion

The inheritance of these hands through a single ontogenic pattern that is at least 370 million years old has allowed a small offshoot of mammals to become the dominant life form on earth.⁵⁴ We have heeded the biblical injunction, "Be fruitful, and multiply, and replenish the earth, and subdue it: and have dominion over the fish of the sea, and over the fowl of the air, and over every living thing that moveth upon the earth."⁵⁵ But we may ask if our handling of our charge has been overzealous and our success too rapid. The rough hands of dominion might be better used as the gentle hands of stewardship. The intelligence gained as a handmaiden should be used to guarantee that our capabilities do not lead to our own inadvertent contribution to extinction (Fig. 12).

Our hands appear and are seen to move in ultrasonographic display within the first few weeks of life. They deteriorate with use and age, but within that span they provide us with dexterity, agility, proficiency, and skills beyond the comprehension of the finest engineering minds. They allow us to manipulate through an array of forces from a gentle pinch to a crushing grasp. They allow the deftness to create music, intricate works of art, and precise technical devices. They hold infants with tenderness and aid the disabled with compassion. They enable the ordering and tallying of commerce from cuneiform marks on Babylonian clay to the keyboards of modern computers. They are all but impervious to mud and motor oil. They callous and thicken with abuse, and they repair most of their injuries without intercession. They are a means of protection and an assurance of modesty. They are vital to emphasize verbal communication, express thanks, or direct derision. They express emotion from the hiding of tears to the touch of compassion. They allow us as surgeons to pursue a calling that rewards us both monetarily and spiritually. The evolution of our knowledge and ability depends on our assessment of results, and for this we

are indebted to our patients for their forbearance. We have the privilege of caring for the most elegant of human parts.

Your pilgrimage to this meeting and others like it signifies your willingness and commitment to remain at the forefront of advancement for the care of the hand. For that I invoke one last function of the hands, and that is to applaud your resourcefulness and dedication. You may have my hand on it.

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Tension band arthrodesis of small joints in the hand

Two-hundred three patients underwent 290 tension band arthrodeses of the metacarpophalangeal and proximal interphalangeal joints of the hand. Nine patients (3%) failed to achieve bony union, four had painless pseudarthroses, and one patient had a small finger amputation. Twenty-five fusions (9%) required hardware removal. There were 10 superficial infections (all responded to oral antibiotic therapy), and three fusions were malrotated. Tension band arthrodesis is our choice for fusion of the metacarpophalangeal and proximal interphalangeal joints. It is reliable and provides stable fixation, pins do not protrude, and external splinting is unnecessary in the cooperative patient. (J HAND SURG 1993;18A:194-7.)

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Small joints of the hand can be altered by arthritis, trauma, contracture, or paralysis with consequent functional impairment. The original insult causes destruction of the articular contour, often with irreparable damage to the soft tissue sleeve. The resultant pain, deformity, and instability are indications for arthrodesis, because arthroplasty may not be feasible or advisable.

Tension band arthrodesis is not new. It was first described by Segmüller¹ in 1977, and subsequent clinical