REVIEW ARTICLE

Evolution of the Shoulder Girdle
with Special Reference to the Problems of the Clavicle

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Abstract Persistent problems involving the clavicle include the reason for its reduction in many mammals, its function in hominids, the last ossification, and so on. In this paper these problems are considered from the point of views of comparative and functional morphology. The clavicle is an element of the dermal shoulder girdle that is in the process of reduction through tetrapod evolution. The reason why the clavicle disappeared or was reduced in cursorial mammals is probably that it disturbed the reciprocal movement of the scapula. The human clavicle works also as a supporter of the forelimb. The characteristic double-curved form of the clavicle may be related to its function. The sternal epiphysis of the clavicle fuses last among the long bones of the human skeleton, in spite of the first ossification of the clavicular body. The delay of determination of the clavicular length should be convenient to slight adjustment for retaining dynamic stability in human bipedal walking.

Key Words: Clavicle, Shoulder girdle, Evolution, Comparative osteology, Functional morphology

Introduction

There is no bone as peculiar as the clavicle among the bones that comprise the human skeleton. It is the only dermal bone in the postcranial skeleton. Its ossification begins first and the sternal epiphysis closes last among the girdle and limb bones. In mammalian forms the clavicles vary in their presence or absence and degree of development. The human clavicle has the characteristic S-shaped double curve of primates. Why is the clavicle so peculiar? Some authors have noted that pectoral and pelvic girdles are serially homologous. Is the clavicle truly homologous to the pubis?

In the present paper I will try to take into account many factors that may help us to get answers to the problems about the clavicle. In order to solve the problems of the clavicle, the shoulder girdle must be considered as a whole. The free limbs must be also considered altogether to understand the girdles. It is necessary to compare humans with other primates in order to understand some features of the human shoulder girdle. The evolution of mammals, reptiles and other vertebrates must be followed to know the derivation of their shoulder girdles. Therefore, under the title "Evolution of the shoulder girdle"
problems of the clavicle are considered, including the pelvic girdle and free limbs.

**Elements of the Shoulder Girdle and Their Evolutionary Trends**

As the shoulder girdle consists of dermal and endoskeletal elements, each element is separately described following ROMER and PARSONS (1977), KENT (1978), WAKE (1979) and STARCK (1979).

The dermal shoulder girdle is derived from the pectoral armor of placoderms. As the crossopterygians took to land, the operculum was lost; the subsequent loss of the posttemporal, which was situated most dorsally among the dermal shoulder girdle elements, resulted in the disconnection of the dermal shoulder girdle from the cranium. The dermal shoulder girdle includes the posttemporal, supracleithrum, postcleithrum, cleithrum, clavicle and interclavicle (Fig. 1). Among these elements, all except the interclavicle were originally present and only the interclavicle appeared after the transition to land (ROMER and PARSONS, 1977). The dorsal elements (posttemporal, supracleithrum, and postcleithrum) are well developed in aquatic forms but tend to be reduced in terrestrial forms. Table 1 shows the presence or absence of the ventral elements (cleithrum, clavicle and interclavicle). According to the table, even the ventral dermal elements have a tendency to become reduced. It is concluded that the dermal elements as a whole have a tendency to become reduced or disappear.

The endoskeletal shoulder girdle lies within and behind the dermal girdle and bears the glenoid fossa (ROMER and PARSONS, 1977). The endoskeletal girdle includes the scapula, procoracoid and coracoid (Fig. 1). The scapula is present above the glenoid fossa, and the others are below it. The procoracoid is also called the epicoracoid and the coracoid is also called the metacoracoid. Table 2 shows the presence or absence of the endoskeletal shoulder girdle.

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**Table 1.** Distribution of features of ventral elements of the dermal shoulder girdle; O: presence, ×: absence

<table>
<thead>
<tr>
<th>Dermal shoulder girdle</th>
<th>Cleithrum</th>
<th>Clavicle</th>
<th>Interclavicle</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crossopterygians and sturgeons</td>
<td>O</td>
<td>O</td>
<td>×</td>
</tr>
<tr>
<td>Teleosts</td>
<td>O</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Ancient amphibians and reptiles</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>Turtles, lizards, snakes, birds and monotremes</td>
<td>×</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>Crocodiles and alligators</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>Dinosaurs</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
<tr>
<td>General mammals</td>
<td>×</td>
<td>O</td>
<td>×</td>
</tr>
<tr>
<td>Ungulates and whales</td>
<td>×</td>
<td>×</td>
<td>×</td>
</tr>
</tbody>
</table>

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According to the table, the scapula never disappears, but instead develops. To the contrary, the ventral elements of the endoskeletal girdle have a tendency to become reduced. The dermal girdle is more developed than the endoskeletal girdle in aquatic fishes and is less developed in terrestrial tetrapods. The reason why such a condition occurred is that the caudal margin of the gill opening must be hardened in fishes and that tetrapods need many more girdle muscles because of the transformation of the main locomotory organ from the trunk to the limbs.

Table 2. Distribution of features of the endochondral shoulder girdle; O: presence, Δ: fuse, x: absence

<table>
<thead>
<tr>
<th>Endochondral shoulder girdle</th>
<th>Scapula</th>
<th>Procoracoid</th>
<th>Coracoid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ancient amphibians</td>
<td>O</td>
<td>O</td>
<td>x</td>
</tr>
<tr>
<td>Early reptiles and birds</td>
<td>O</td>
<td>O</td>
<td>x</td>
</tr>
<tr>
<td>Mammal-like reptiles</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>Monotrems</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>Marsupials and eutherians</td>
<td>O</td>
<td>O</td>
<td>Δ</td>
</tr>
</tbody>
</table>

Finally, no matter what the actual ossification pattern is, the clavicle of eutherians, including humans, is truly homologous to the original dermal shoulder girdle. The reason why only the clavicle among the postcranial skeleton derives from dermal bone is that only one bone survived among the many original dermal elements, and that the clavicle was originally a part of the dermal cranium in spite of being a part of the “shoulder girdle” in human anatomy. As MIKI (1981) expressed it, “the dermal shoulder girdle was a remnant of the posterior margin of the helmet in armored fishes.”

The Evolution of the Shoulder Girdle in a Functional View

1. Early tetrapod stage: lateral type limb

The early tetrapods and amniotes have laterally oriented limbs. REWCASTLE (1981) calls it “sprawling limb posture”. The “lateral” type limb is also called the “horizontal” or “transverse” type. LESSERTSIEUR and SABAN (1967) separate the advanced “type horizontal” from the more primitive “type transversal”, but I unite them as the lateral type; they are common in having the stylopodium protruding horizontally from the trunk. Bodies with the lateral type limb develop adductor muscles which run from the ventral part of the joint of girdles to the humerus and femur in order to bear the trunk off the ground. The amphibians and early reptiles walk by moving both stylopodia fore-and-aft in a horizontal plane for their lateral type limbs. This
movement enlarges the area of muscles in the pelvic girdle which protract and retract the limbs.

Thus, in both girdles the area ventral to the joint with the stylopodia becomes broader than the dorsal area, and the area anterior to the joint extends forward and the posterior area backward. “Both pectoral and pelvic girdles can be reduced to a common pattern, of one dorsal and two ventral elements” (YAPP, 1965). Therefore, the clavicle is not homologous to the pubis but analogous to it.

While the shoulder and the pelvic girdles converged on a common pattern, they were to take a contrasting shape in their connection with the axial skeleton because of the presence of the thorax. That is, the shoulder girdle unites with the thorax via the clavicle or the interclavicle (lost later and changed to the sternoclavicular joint), and the pelvic girdle unites with the sacrum via the ilium by a bony connection. The shoulder girdle forms a striking contrast to the pelvic girdle in the relative position of its bony connection between the axial skeleton and the articulation with the limbs: it is more ventral in the shoulder girdle and more dorsal in the pelvic. In other words, the body weight hangs from the shoulder girdle in the anterior half of the body and rides on the pelvic girdle in the posterior half. This point is one of the factors that later differentiates the shoulder and pelvic girdles in shape.

2. Mammal stage: inferior type limb

A typical mammal has limbs of the “inferior” type. It is also called the “parasagittal” or “vertical” type, and is a body form in which the stylopodia extend beneath the trunk. REWCASTLE (1981) calls it “erect limb posture”. This posture had already been gained in some “mammal-like reptiles”. How did the lateral type limb become the inferior type? A transformation from the lateral to the inferior type limb is not simple; the toe tips point outward in the lateral type. Actually the transformation was established by rotation of the elbow backward and of the knee forward.

There have been some theories about the reason why the stylopodia in fore- and hindlimbs rotated in opposite directions: for example, in an animal that extends its limbs outward from the trunk, it is dangerous when a predator attacks, or it conserves body heat to hold the limbs under the trunk, or it is better for walking on narrow branches (MATTHEW, 1904; GREGORY, 1910; BÖKER, 1935). But amphibians and reptiles retain the lateral type limbs even now, notwithstanding the presence of many predators. It does not seem to have been so cold as to require the animals to conserve body heat, when and where the “mammal-like reptiles” evolved the inferior type limbs. And there is no evidence that they were arboreal animals.

The most important reason for the transformation from the lateral to the inferior type
limb is to bring the contact points of the feet to the ground toward the center of gravity of the body (Fig. 2). This theory is preferable, because it explains with a single reason not only that the distance between each foot becomes narrow but also that the distance between fore and hind feet becomes narrow. Thus the fore and hind stylopodia rotated in opposite directions.

SWINNERTON (1923) and RADINSKY (1987) very simply noted this the "gravity center approach theory" in spite of the presence of some different theories mentioned above. I happen to have the same opinion as his, and not only support the theory but will emphasize its significance more and more, because I believe that the transformation to the inferior type limb played the most important role in the evolution of later mammals and in the differentiation of fore- and hind limbs in shape. For example, along with the inferior type limb can be explained the rise of the elbow, knee and heel peculiar to mammals.

When the limb type transforms from lateral to inferior, the direction of the long axis of the stylopodium approaches the direction of gravity, and so the role of muscle decreases in its support of body weight, while the body weight that can be supported by muscles of the same quantity increases. Therefore, body size can enlarge and limb bones elongate to heighten the center of gravity of the body. A high position of the center of gravity brings better moving ability instead of stability. Unstable posture would develop a reflex tract of the nervous system and balance function of the brain, which will raise the efficiency of movement more and more. Thus mammals finally achieved a high level of function of movement and a larger brain. Dinosaurs independently evolved the inferior type limb, while amphibians and other reptiles retain the lateral type limbs for adaptation of stability.

When the limb type changed from lateral to inferior, the limb girdles also changed. As the elbow rotated backward and the knee forward, the humerus inclined forward and the femur backward, and so the scapula inclined backward and the ilium forward. There have been different opinions about the reason why the dorsal elements of the girdles which extended upward in the animals with the lateral type limb were oriented in such a way. BÖKER (1935) assumed an arboreal animal as a primitive type for mammals and thought that the fore- and hind limbs and the axial skeleton would comprise an arch as a whole to support the body weight of the animal. So, he illustrated a scheme like Fig. 3. BABA (1984) attributed the angle of forward inclination of the pelvic girdle to the direction of a resultant of anti-gravitational direction in standing and thrust direction in moving. But the inclination of the scapula cannot be explained with this opinion, and BÖKER’S view includes only a support function in standing, not in moving. To explain the inclination of the girdles, a theory is more desirable by which both fore- and hind limbs in both standing and moving positions can be explained.

Now, a translation from the lateral to the inferior type of limbs brought the muscles much alteration. In an animal with the lateral type limb three kinds of muscles were necessary: adductor muscles to pull inward the stylopodium under the joint for support of the body weight, retractors for thrust, and protractors for recovery. When an animal with the inferior type limb advances, it is enough to move the limbs fore-and-aft in the sagittal plane. As a result, the same muscles could

![Fig. 3. Bow structure in mammalian skeleton. After BÖKER (1935).](image)
work for support and progression. An extensor that passes before the shoulder joint or behind the hip joint, should be able to play a role of supporting body weight in the “inferior” type animals.

Dorsal and ventral elements of the girdles are markedly different except that they are situated dorsally and ventrally to the joint. The ventral element extends inward to the joint, rather than just downward, and tends to join with another element in the median plane. On the other hand, the dorsal element extends upward and never joins with another. The ventral element from which the adductors originate is suited to support the body weight in an animal with the lateral type limb, and the dorsal element that extends sagittally is suited for muscle attachment that extends and flexes the inferior type limbs.

In an animal with the inferior type limb the body weight is distributed so that the limbs are flexed. That is, the body weight is distributed so that the humerus inclines more forward because it is set to be inclined anteriorly and the femur more backward because it is set to be inclined posteriorly. Therefore, it is important for the muscles to pull the humerus forward in the shoulder girdle and the femur backward in the pelvic girdle in order to support the body weight.

To pull the humerus forward (extend the shoulder joint) the development of the supraspinatus and deltoideus is necessary and this develops the supraspinatus fossa of the scapula and the deltoid ridge of the humerus. To pull the femur backward (extend the hip joint) the development of the gluteus medius and biceps femoris muscles is necessary and this develops the gluteus surface and the ischial tubercle of the hip bone. As a result, the dorsal elements of the girdles, scapula (GREGORY, 1912; WOLFFSON, 1950) and ilium are enlarged in animals with inferior type limbs, while the ventral elements are reduced with loss of the support function of the adductor muscle.

The clavicle, a ventral element of the shoulder girdle, varies in its degree of development among mammals and is completely lost in many forms. Table 3 shows the presence, absence or degree of reduction of the clavicle in each order according to LESSERTISSEUR and SABAN (1967). Looking at the ordinal distribution from the point of view of life style, the clavicle is very important in forms in which the anterior limbs move in three dimensions (the flyer, the glider, and the climber), except primitive monotremes and insectivores. On the other hand, fully aquatic and cursorial forms lose their clavicles. In cursorial carnivores, the clavicle is present as a remnant, but is buried in the tendon and does not work as a brace of bone. Less specialized forms, such as marsupials, rodents and edentates, retain the clavicle and some of them lose it. Accordingly we can conclude that the clavicle generally is reduced or lost in cursorial or aquatic forms.

There have been several views about the cause

<table>
<thead>
<tr>
<th>Present</th>
<th>Partly absent or reduced</th>
<th>Absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monotremes (primitive)</td>
<td>Marsupials (absent in Perameles)</td>
<td>Pangolins (fossorial)</td>
</tr>
<tr>
<td>Insectivores (primitive)</td>
<td>Rodents (absent in Capybara)</td>
<td>Whales (aquatic)</td>
</tr>
<tr>
<td>Bats (volant)</td>
<td>Carnivores (cursorial)</td>
<td>Sirenians (aquatic)</td>
</tr>
<tr>
<td>Primates (arboreal)</td>
<td>Rabbits (cursorial)</td>
<td>Proboscideans (graviportal)</td>
</tr>
<tr>
<td>Flying lemurs (glider)</td>
<td></td>
<td>Coneys (terrestrial)</td>
</tr>
<tr>
<td>Aardvarks (fossorial)</td>
<td></td>
<td>Perissodactyls (cursorial)</td>
</tr>
<tr>
<td>Edentates (fossorial)</td>
<td></td>
<td>Artiodactyls (cursorial)</td>
</tr>
</tbody>
</table>
of the clavicle's reduction. HILDEBRAND (1960) noted the advantage of no clavicle, which however may not be a cause of it: "In the carnivores this freedom is increased by the reduction of the collarbone to a vestige; in the ungulates the collarbone is eliminated." ROMER (1966) also noted, "The clavicle disappears, thus freeing the shoulder from any bony connection with the body breaking the jar of landing on the front feet after a bound." LESSERTISSEUR and SABAN (1967) said; "Reduction of the clavicle may be related to decreasing of pressure of the forelimb." YOUNG (1975) said, "the forelimb retains greater freedom than the hind and has tended to acquire other functions...the region to which the forelimb is attached (the thorax) must participate in respiration, necessitating independent movements. For all reasons, therefore, power to move the limb in various directions is more important than firm attachment..." ROMER and PARSONS (1977) said, "complete freedom of the shoulder blade from the body skeleton is desirable to relieve the jolts transmitted from front legs to body and to increase the functional length of the limb...".

A bony connection between the pelvic girdle and the spine, however, is not lost in bipedal forms to absorb the shock and to progress using only the hind limbs. In most mammals the body weighs more on the forelimbs than on the hind limbs. The more function the forelimb has, the more developed is the clavicle. It is hard to attribute advantages without the clavicle to the original cause of reduction. Therefore, in considering the cause of clavicle reduction, a theory that does not contradict the life function of living forms should be chosen, and disadvantages for life with the clavicle rather than advantages without the clavicle should be looked for in order not to fall into teleology.

Limb bones lengthen in mammals that are adapted for running. Specifically, the stylopodia, zeugopodia and metapodials lengthen, and in the proximal portion of the forelimb the scapula lengthens to become a functional part of the limb. In this case, because the first limb segment of the forelimb inclines oppositely to the corresponding segment of hind limb, for the reason mentioned above, the scapula corresponds to the femur functionally (Fig. 4). This idea occurred to me while I thought about the reason of clavicle reduction (INUZUKA, 1988), but EATON (1944) had long since noted the correspondence between the forelimb plus scapula and the hind limb, and BABA (1988) probably got the same idea independently without referring to the work as well.

In other words, the scapula tends to move anteroposteriorly in the sagittal plane, like the femur. At this time, the acromial end of the clavicle, which connects the sternum to the scapula, draws a locus of an arc with an axis revolving about the sternoclavicular joint and produces horizontal component, so the presence of the clavicle must be an impediment for the scapula to try to reciprocate sagittally (Fig. 5). I think that an experiment using a aclaviculate rat (JENKINS, 1974) proved this explanation. As a result, the clavicle would begin to reduce first from both articular ends to abandon its function.

Fig. 4. Fore- and hind limb segments with opposite inclination in mammalian skeleton; broken line: analogy in both limb segments, dotted line: homology in both limb segments. The elbow corresponds to the heel functionally.
The presence of the clavicle which draws a locus of an arc (left), which interrupts the movement of the scapula as it tries to reciprocate sagittally (right). This condition is shown in some carnivores. It seems that the clavicle has become progressively more reduced to become lost completely in ungulates.

3. Primate stage: brachiation

The shoulder girdle of the primates, particularly of the apes, has been investigated in detail for a long time (MIVART, 1867; AEBY, 1878; MOLLISON, 1911; BOLTZE, 1926; FICK, 1926; SCHULTZ, 1926, 1930, 1937; WATERMAN, 1929; MILLER, 1943; INMAN et al., 1944; SMITH and SAVAGE, 1955; ASHTON and OXNARD, 1964a, 1964b; OXNARD, 1967, 1969; ROBERTS, 1974; JENKINS et al., 1978). However, a few functional studies of the clavicle have been done. Arboreal primates have various modes of locomotion: vertical clinging and leaping in prosimians and brachiation and knuckle walking in apes, as well as a quadrupedal walking on the ground and in branches. Among these, brachiation is considered here, because it is developed in apes.

The importance of the clavicle to connect the sternum with the scapula is great because brachiators must bear the body weight by the forelimb. In the brachiators the clavicle reaches its greatest length (MILLER, 1932). In order to increase the range of reach of the forelimb, a more mobile clavicle acting as part of a free limb is favourable, that is to say, the center of forelimb movement is transferred from the shoulder joint to the sternoclavicular joint. Thus, the clavicle of primates, particularly apes, is developed as the most proximal segment of the forelimb (Fig. 6).

In cursorial mammals the scapula itself also rotates, that is, "the shoulder blade pivots from about midway in its length, and the shoulder joint at its lower end is free to move forward and backward with the swing of the leg" (HILDEBRAND, 1960). The shoulder girdles of both primates and cursorial mammals are common in having the center of forelimb movement off the shoulder joint: the sternoclavicular joint on the one hand and the scapula on the other. Thus, generalizing the points of view that the scapula of cursorial mammals and the clavicle in primates are functionally incorporated into the limbs, a concept "freelimbization" of the shoulder girdle is obtained. The shoulder girdle, which originally filled the role of connecting the axial with the appendicular skeleton, changed its main function from supporting to moving as each animal
adapted itself to distinctive modes of locomotion, terrestrial running or brachiation among branches in forests. By the way, while the clavicle is lost in ungulates in which the scapula is "free-limbized", why is the scapula not reduced in primates in which the clavicle is "free-limbized"? There are three presumed reasons: the scapula cannot be lost because of the glenoid cavity which must articulate it with the humerus; the scapula develops as an attachment area of the shoulder girdle muscles; the acromion develops as a part to articulate with the clavicle.

Such a long clavicle in primates is very convenient for locomotion among branches, but may prevent the forelimb from reciprocating sagittally during quadrupedal locomotion for the reason mentioned above. The least possible load on the forelimb would be better for the shoulder joint which shakes side by side with every step in its horizontal component. This condition may be related to the gait peculiar to primates (Hildebrand, 1967) that make them different from other mammals.

4. Hominid stage: erect bipedal walking

Many authors have referred to the function of the hominid clavicle. Holden (1855) said, "Its chief use is to keep the shoulders apart, that the arm may enjoy a freer and wider range of motion. By moving the shoulder, you will find that the clavicle acts as a prop, the fixed end of the prop being at the sternal joint." Todd (1937) said, "Its mechanical function is to give side support to the shoulder joint for the wide and varied movements of the arm. It acts like a yard-arm, keeping the shoulder joint free from the chest, and has a definite though limited action in itself." Yapp (1965) said, "Where, as in man, the arm can be moved inward, the clavicle or collar-bone is large. If it were not present, contraction of the breast muscles, instead of rotating the humerus round the glenoid cavity, would simply pull the whole shoulder inward." Breathnach (1965) also said, "...thus functions that call for lateral motions in the limb require a clavicle to support the scapula." Campbell (1966) said, "The clavicle maintains the distance of the scapula from the sternum and, acting as a strut, allows movements of the scapula at a constant radius from the manubrium." Moseley (1968) noted several functions of the clavicle, as follows: 1) It acts as a rigid base for muscular attachments; 2) It forms a strut holding the glenohumeral joint in the parasagittal plane; 3) It increases the power of the arm-trunk mechanism in certain areas of motion; 4) It provides a protection for the major vessels; 5) It serves a cosmetic function. Sinclair (1970) said that its function was "to thrust the shoulder joint away from the trunk so that the arm can move freely without being obstructed by the thorax." Bass (1971) said, "Its function is to act as a strut or prop to the shoulder, thereby holding the scapula and upper limb laterally, backward and slightly upward." Akashi (1973) said, "because missing clavicles doesn't obstruct one's life, the clavicle works to guard blood vessels and nerves and as an attachment of supplementary muscles of respiration." Shipman et al. (1985) said, "The major function of the clavicle is to hold the shoulder joint and the upper limb away from the thorax, permitting free movement of the limb."

All these explanations are not wrong, but it doesn't seem that they are sufficient to interpret the form of the hominid clavicle functionally. The function of the clavicle to keep the shoulder joint at a certain distance from the sternum is common not only to hominids but to mammals with non-reduced clavicles. For example, Le Gros Clark (1971) noted, "This bone, ... serves as a strut which, ... allows free movements of the limb away from and towards the body" or Ewer (1973) said, "The main function of the clavicle is to stabilize the lower end of the scapula.
during abduction of the arm ....” This function should be seen as inherited from primates rather than one unique to hominids. The hominid clavicle has most remarkable double curvature (Fig. 7). “A sigmoid vertical (in Man horizontal) curvature is not generally well marked; it is most so in Man, ... the sternal curvature is much less than in Man, even in Troglydytes and Simia” (MIVART, 1867). And “the lateral end of the clavicle lacks the pronounced cranial twist that characterizes it in the apes” (AIELLO and DEAN, 1990). These features should be considered from the peculiar functions of the hominid clavicle that make it different from those of other primates, especially other apes.

The mode of locomotion of apes is primarily characterized by brachiation among trees and knuckle walking on the ground, whereas that of hominids is erect bipedal walking. Let us consider the effect that this change of mode of locomotion has on the shoulder girdle, especially the clavicle. The clavicle of apes is primarily acted on by body weight both in walking and in brachiation: each clavicle is under the influence of the whole body weight in brachiation and both clavicles are forced to carry the weight of the upper half of the body in knuckle walking. OXNARD (1984) noted that the clavicle bore the tensile forces. On the other hand, hominid upper limbs became free with erect posture, so that the shoulder girdle switched its role from support of the body weight to support of the free upper limbs.

The free upper limbs are not supported only by bones of the shoulder girdle, scapula and clavicle. If only these bones supported them, the clavicle would work as a cantilever and bear bending stress. I think that co-operation of the clavicle and trapezius muscle is rather important. The trapezius muscle originates broadly from the cranium and the spinous processes of the cervical and thoracic vertebrae and converges to insert on

![Fig. 7. Clavicles of man and apes. From left to right, sternal end, cranial view, and acromial end. Drawn to scale except for Hylobates (× 2)](image-url)
the clavicle and the scapular spine. Among the muscle bundle the part that originates from the highest position, the cranium, mainly works as a support of the free limb. This is evidenced by the exceptional thickness of the free edge of the human scapular spine. Fig. 8 shows their relative position schematically. The figure is reminiscent of a crane; the clavicle and trapezius muscle work co-operatively as an arm and a cable of a crane to hang the free upper limb. In this situation the load of the free upper limb must be borne by tension in the trapezius and compression in the clavicle.

Thus the freeing of the forelimb with erect posture in hominids must have converted the clavicle's main function to rather compression than tension or bending. I suspect that this conversion compressed the clavicle from side to side to make a double-curve, sternal and acromial curve, most distinctive in man. By the way, the idea that bones respond to plastic deformation in the short term of phylogeny is obtained from observation of the parietofrontal crest of NAUMANN's elephant (INUZUKA, 1977) and of the tibia of Desmostylus (INUZUKA, 1984).

According to MOSELEY (1968), "This position of the clavicle is characteristic to each individual and shows considerable variation. An upward slope of 10° to 12° from the horizontal is a fair average." There should be an optimum angle at a position a little above the horizontal so that the stress is equally distributed through the cross section of the clavicle. If the idea that the human clavicle is under compression is true, this idea could explain also the slope of the clavicle.

When a man walks, the torsion of pelvis by the fore-and-aft swing of the lower limbs is
negated by the reverse torsion of the shoulder by
the reverse swing of the upper limbs. This is called
the dynamic stability of the bipedal walking (Fig.
9). The quantity of moment is given by a pro-
duct of the mass and the moment arm length. The
reason why the moment of the upper limb is
balanced by one of the lower limb, which is much
heavier than the upper limb, is that the shoulder
width is larger than the distance across the
acetabula. As one grows older, the length and
weight of the upper and lower limbs increase. The
growth of limb bones in length ends with the
fusion of the epiphyses. The clavicle ossifies
earliest among all limb bones and its sternal
epiphysial line closes last. The free limb bones
of the upper and lower limbs close their epi-
physial line to setting the approximate weight of
adult limbs during the later term of puberty. Even
if the free limb increases just a little in length,
it increases by a cube in mass. Therefore it ought
to be more effective to adjust the moment arm
length than the mass in order to balance the
moment of upper limbs with that of the lower
limbs. This is presumably a reason why the
clavicle closes its sternal epiphysis last, which
delays the decision of its length than any other
free limb bones.

Postscript

I introduce and criticize previous theories and
propose my opinion about some problems of the
shoulder girdle, especially the clavicle, in the
present paper. My opinion shown here is not
definitive and is only a tentative idea from a point
of view of comparative and functional morpho-
logy. I know of possible objections to many
points but my goal in publishing it here is to
stimulate further discussion.

I would like to thank Prof. Banri ENDO of
the University of Tokyo for his helpful advice and
a critical reading of the manuscript. I sincerely
thank Prof. Morihiko OKADA of the University
of Tsukuba, Editor-in-Chief of this Journal, for
giving me a chance to submit. I am grateful to
Dr. Tasuku KIMURA of the Primate Research
Institute of Kyoto University for giving me a
chance to give a talk in the Hominization
Research Association. I also thank Dr. Nobutoshi
YAMAZAKI of Keio University and participants
of the Association for discussion and many
suggestion.

I thank Prof. Kevin PADIAN of the University
of California, Berkeley and Dr. Gen SUWA of
the University of Tokyo for checking my English
manuscript. I also thank Dr. Howard HUTCHI-
SON of the Museum of Paleontology, University
of California, Berkeley and the Agassiz Museum
of Harvard University for giving me access to
specimens of mammalian clavicles for compari-
son.

抄　録

肩帯の進化－鎖骨を中心として－

犬塚則久

鎖骨は特異な骨である。例えば、真獣類のからだの
骨では唯一の皮骨性骨である。哺乳類の中で退化した
ものと発達しているものとがある。ヒトの鎖骨は二重
彎が最も強い。骨化点出現は早いのに胸骨端の発着
は骨の中で最も遅い。これからの理由を探るため、肩帯
の進化を比較解剖学的および機能形態学的観点から検
討した。

皮骨性肩帯は四足動物では全般に退化傾向にある。
皮骨性肩帯の実体は皮骨性頭蓋の後継であり、鎖骨は
その最後の名残である。肩帯と腰帯は同物ではなく、
側方型体肢をもつ四足動物の祖先が獲得した相似形
象である。体肢が側方型から下方型へ転換したのは、足
の接地点を重心に近づけるため、この結果、肘は後
ろ、膝は前に回転することになった。これが哺乳類に
おける前・後肢の形態差の発端で、肢帯や基脚の逆傾
斜、肘・膝・鎖の出現を説明する。哺乳類の肩帯は「自由肢化」し、行
走性哺乳類では肩甲骨の自由肢化が鎖骨の退化を促した。一方、樹上性哺乳類では鎖骨
が自由肢化し、新たな機能を獲得したために、皮骨性
肩帯の退化傾向から一転して発達するようになった。
References


