" A CONTRIBUTION TO THE FUNCTIONAL MORPHOLOGY OF THE MAMMALIAN CARPUS."

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Derek William Yalden, B.Sc.

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EXTRACT

While the positional relationships of the mammalian carpal bones were fully discussed by palaeontologists around 1900, the dynamic role of the carpus has been almost ignored.

The roles of the forelimb in locomotion and of the carpus within the forelimb are briefly considered. There is a tendency for the wrist to be rigid during retraction, in contrast to the activity of the tarsus, and it acts as a hinge only when the limb is off the ground, folding the limb during protraction. The position close under the mid-line in which the feet are placed is emphasised, since this means that the lower limb segments must swing out sideways to pass the contralateral limb. Some ulnar deviation must accompany flexion at the carpus to achieve this.

The form and function of the carpus in various groups of mammals is examined. Function is determined largely by manipulative studies, and described as degrees of flexion and deviation at the two main carpal joints. Thus in Carmivora, the proximal joint is both the main flexion hinge and a deviational joint, while the mid-carpal joint is solely a flexion hinge. In these and many other quadrupedal mammals with proximal joints of similar function, the scaphoid and lunar bones of the primitive carpus are fused. In ungulates, both joints are solely flexion hinges, and the bones of the proximal row must remain separate to provide the twisting movement which gives the deviational component. In primates both joints give moderate flexion and deviation. The isolated position of the Monotremes is emphasised.

CONTENTS

Section 1 : General Considerations	
Introduction	170 5
Descriptive Terminology	6
Composition of the Carpus	8
Variability in the Mammalian Carpus	12
Propulsive Functioning of the Mammalian Limb	13
Plantigradism	21
Dual Function of the Carpus	22
Limb Position	25
Section 11 : Systematic Survey	
Methods and Materials	33
Key to Diagrams	40
Carnivora - Fissipedia	41
Carnivora - Pinnipedia	58
Ungulate Groups	72
Subungulata	93
Primates	108
Edentata (Xenarthra)	122
Pholidota and Tubulidentata	142
Rodentia	149
Lagomorpha	156

Insectivora	160
Chiroptera	176
Dermoptera	181
Marsupialia	183
Monotremata	194
General Discussion	203
Acknowledgements	215
Bibliography	216
Appendix: Table of Measurements	224
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GENERAL CONSIDERATIONS

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Previous work on the mammalian carpus has mostly been of a descriptive nature contained either in a general anatomical or palaeontological account. There are therefore innumerable superficial accounts of the carpus in one mammal or another, giving the names of the bones present and perhaps the appearance as might be seen in a mounted skeleton. This information is summarised by Flower (1885) and in the volumes of Grassé (1955). Several workers, notably Osborn (1890, 1929) and Matther (1897, 1909), have given additional emphasis to the positional relationships of the carpal bones, particularly in discussing the primitive arrangement in ungulates.

Truly functional studies, however, are rather few, and only for the human carpus is there an extensive literature. Among the more important papers are Johnston (1907), investigating the arrangement of the carpal bones in different positions of the wrist by dissection, Virchow (1899) using plane X-rays and Wright (1935) using various techniques including stereo-X-rays. The contribution of Gilford, Bolton and Lambrinudi (1943) adds a valuable mechanical interpretation. For other animals, previous work is rather slight; Sisson and Grossman (1953) give an account of the movements of the carpal bones in the horse, and Backhouse (1961) considers both form and function of the carpus in the seal. The present account attempts to extend knowledge of carpal function and its relationship to the shape of these bones on a comparative basis.

DESCRIPTIVE TERMINOLOGY

("palm-up"

One of the problems of comparative anatomy is the differences encountered in the terminology used, particularly between medical and zoological literature. Further, one must find terms which remain useful whether one considers the upright limb of a horse or the laterally placed forelimb of a mole. Table I below shows the descriptive terms which have been used and the most frequently encountered synonyms from previous, mostly medical, literature.

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the mid-line or to one mother. Thus the digits are adjucted when agreed,

Table I - Descriptive terms

Present Account	Synonyms
Proximal occurs in the directi	Superior, Above and
Distal dose"); following Gray	Inferior, Below
Ulnar (Ulnad)	Medial, Minimal
Radial (Radiad)	Lateral, Pollicial
Extensor (Extensad)	Dorsal, Posterior
Flexor (Flexad)	Palmar, Volar,

Pinelly, there are the terms used to dealers Ventral, Anterior

The use of these particular terms avoids such anomalies as the "anterior" surface in human anatomy being that which in most, quadrupedal, mammals faces posteriorly, and also leaves the usual directional terms to refer to the orientation of the animal as a whole. Thus the flexor surface of the manus in the mole, <u>Talpa</u>, may be said to face posteriorly, the radial border is directed ventrally. In the usual terms of anatomy, the anterior surface

faces posteriorly, and the lateral surface ventrally.

The terms used to describe the movements occurring at the wrist are more generally accepted. In the usual antero-posterior plane the movements are described as flexion or extension, with the straight position as in extension". Movements beyond this position in the same plane may be described as dorsiflexion or hyperextension; the latter is generally preferred here since the movement is produced by the extensor muscles. Movements in the radio-ulnar plane are described as deviation, either ulnar or radial. The terms adduction and abduction are sometimes used for these movements but are here used only for movements of the digits relative to the mid-line or to one another. Thus the digits are abducted when spread, adducted when closed together. There appears to be no generally used term for the movement which occurs in the direction of pronation to supination ("palm-up" to "palm-down"); following Gray's Anatomy (Johnston et al. 1958) this may be termed axial rotation. In man and most other mammals this is not a movement of the carpus, but is produced between the radius and ulna; in others it may be produced as a combination of flexion with deviation. In a few cases axial rotation occurs as a distinct carpal movement.

Finally, there are the terms used to designate the pose of the limb in various mammals. These terms, though widely used, are rarely defined precisely, and have in any case changed their meanings considerably since first used by Cuvier (1800) to designate suborders of his order "Carnassiers".

Plantigrade or "flat-footed" is used to describe limbs in which the whole of the foot is approximately parallel to the ground. In this position, weight is transmitted through the ankle or wrist bones as well as through the heads of the metapodials and through the toes. The hind foot of man or a baboon is

a good example of this type.

Digit grade is used for those limbs borne on tip-toe. Here the weight is transmitted through the heads of the metapodials and the toes only, the carpus or tarsus being clear of the ground. The feet of the cat and dog are typical examples.

Unguligrade is applied to those animals where weight is borne only by the distal (=ungual) phalanx and perhaps the hoof around it. The horse and ox provide the classical examples.

Some subdivisions are occasionally used; in particular, certain ungulates, the rhinoceros, elephant and hippopotamus being examples, have the limb skeleton in a typically unguligrade position, but get added support from a fibrous pad developed on the flexor side of the foot behind the hooves. These are often termed subunguligrade.

COMPOSITION OF THE CARPUS

Most workers accept that the primitive mammalian carpus consisted of eight bones, plus the pisiform which is usually regarded as a sesamoid developed in the tendon of the <u>flexor carpi ulnaris</u> muscle (Flower, 1885; Romer, 1945). Using the names usually accepted in mammalogy, these bones are arranged as a proximal row of three, the scaphoid (radially), lunar, and cuneiform; and a distal row of four, the trapezium (radially), trapezoid, magnum, and unciform. The eighth bone, the centrale, is placed between these two rows, usually distal to the scaphoid and lunar, proximal to the trapezoid and magnum. The scaphoid and lunar usually articulate proximally to the radius, the cuneiform to the ulna. The trapezoid, trapezium, and magnum bear metacarpals one, two and three respectively on their distal surfaces, while the unciform bears metacarpals

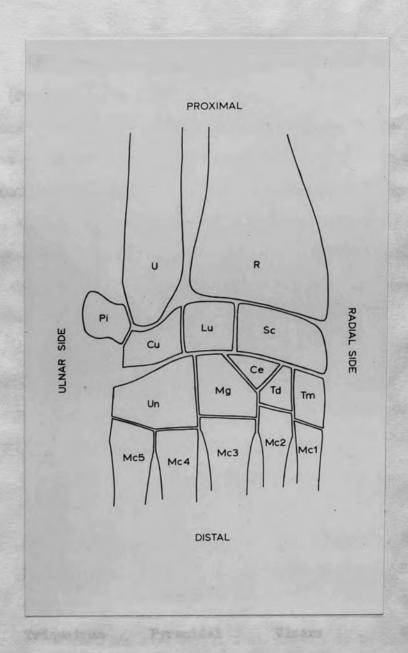


Fig. 1 Diagram to show the composition of the carpal region in a generalised mammal skeleton.

The carpus is bounded proximally by the $\underline{\text{ulna}}$ (U) and $\underline{\text{radius}}$ (R), distally by the five metacarpal bones (Mcl - Mc5).

The carpal bones form two rows. The proximal row includes the <u>cuneiform</u> (Cu), <u>Lunar</u> (Lu), and <u>scaphoid</u> (Sc).

The distal row includes the unciform (Un), magnum (Mg), trapezoid (Tm), and trapezoum (Tm).

Additionally, between these two rows, there is a <u>centrale</u> (Ce); and on the ulnar side of the carpus there is an enlarged <u>sesamoid</u> bone, the <u>pisiform</u> (Pi).

four and five (fig. I). The manage could be used, as having the side at

These bones have been the subject of various nomenclatures. The names used above were originally used in human anatomy and were later applied in comparative anatomy. They have remained in wide zoological usage and so are retained here, despite the fact that medical literature now conforms to the Basle Nomina Anatomica of 1895 and its successor the Nomina Anatomica Paris (1955). As Jones (1944) points out, the B.N.A. is more cumbersome and no more precise than the old terminology.

There are additionally what Jones terms the morphological names, usually used to describe the carpi of reptiles and amphibians. The names used here and usually accepted synonymies are indicated in the following table 2.

p. 95, and fig. 12, p. 10%). The homology of the convictors with a centrale,

Table 2 - The Names of the Carpal Bones

Used Here	B.N.A.	Other Medical	Morphological	Holmgren
Scaphoid	Navicular	fused to ulna"	Radiale	Radiale
Lunar	Lunatum	of the radius.	Intermedium	Centrale I
Cuneiform	Triquetrum	Pyramidal	Ulnare	Centrale 4
Centrale	matemata acc		Centrale	Centrale 2+3
Trapezium	Multangulum	Teyuk, 1933) have	Carpale I	Carpale I
parpal bone, By	majus	osition, flexed o		and the time,
Trapezoid	Multangulum	part in trensmitt	Carpale 2	Carpale 2
Limb skelaton, ne	minus	my significant p	art in directing	
Magnum	Capitatum	of the flexor car	Carpale 3	Carpale 3
Unciform	Hamatum	Uncinatum	Carpale 4+5	Carpale 4+5

While the morphological names could be used, as having the widest zoological applicability, this would imply homology of the mammalian bones with those of the lower tetrapods. Unfortunately, these homologies are controversial, particularly in view of Holmgren's (1952) work. This author doubts, on embryological evidence, the equivalence of the lunar with the intermedium and of the cuneiform with the ulnare. The intermedium he believes to be lost from the proximal edge of the carpus, or reduced to a vestige which may be enveloped in the scaphoid. There is some fossil evidence for this view, for the therapsids Lycaenops and Aelurognathus appear to show the intermedium placed between the distal ends of the radius and ulna, and a larger bone, a centrale, in about the position of a mammalian lunar (Piveteau, 1961, fig. 5, p. 95, and fig. 12, p. 104). The homology of the cuneiform with a centrale, rather than with the ulnare, seems very unlikely on palaeontological grounds, since there is no evidence for the fusion of the ulnare with the ulna in the known fossil series, as is required by his theory. Holmgren's own diagrams seem to suggest that his "ulnare fused to ulna" is a normal distal epiphysis for the ulna, equivalent to that of the radius.

The status of the pisiform as a carpal bone remains to be discussed. While most modern anatomists accept this bone, as suggested earlier, to be a sesamoid, some accounts (e.g. Nayuk, 1933) have considered it to be a "true" carpal bone. By virtue of its position, flexad of the cuneiform and the ulna, the pisiform plays little or no part in transmitting compression through the limb skeleton, nor does it play any significant part in directing movement. It does, however, carry the tendon of the <u>flexor carpi ulnaris</u> muscle across the carpus at a point where, due to the shape of the bones, a smooth running

surface could not be provided; it also, perhaps, allows more leverage to be applied at the metacarpal insertions. Additionally, particularly in the plantigrade, laterally directed foot of a reptile, this is a point at which some pressure from the ground may act on the tendon. The pisiform is certainly a bone of long phylogenetic standing, being evident in the earliest known reptile carpi, such as <u>Dimetrodon</u> (Piveteau, 1961, fig. 27, p. 59), and in most modern reptiles as well as mammals. It is therefore not surprising to find that extra articulatory facets have been evolved, in some circumstances, as in <u>Daubentonia</u> described by Nayuk. The bone has been largely ignored in the account which follows, since it plays no significant part in the activities described.

VARIABILITY IN THE COMPOSITION OF THE MAMMALIAN CARPUS

The idea of a generalised mammalian carpus based on eight bones has been deduced largely from comparative osteology, together with some embryological evidence. All eight bones are present as separate entities in the majority of Primates, in Lagomorpha, and in some Inectivora (e.g. Talpidae, Macroscelididae). More usually, however, the number is reduced through fusion, or disappearance, of bones. The centrale is the bone most usually absent - it is never present in the Perissodactyla or Artiodactyla, and only discernable in the embryo Proboscidea (Eales, 1929). The African anthropoids, Pan and Gorilla, and the Hominidae have the centrale fused to the scaphoid. In the Carnivora the centrale is similarly not apparent, but from embryological (Flower 1871, Leboucq 1884) and palaeontological (Matthew 1909) considerations is known to be fused to the scaphoid and lunar to give a composite scapholunar bone. Some Insectivora

(Soricidae, Erinaceidae) resemble this condition. Lastly, in some other Insectivora (Tupaiidae, Tenrecidae), while the centrale is present as a separate bone, the scaphoid and lunar have fused; the majority of Rodentia has a similar carpus.

The functional background for these different patterns has apparently not been considered before and is emphasised in this study.

PROPULSIVE FUNCTIONING OF THE MAMMALIAN LIMB

Some knowledge of the function of the forelimb is required to understand the role of the carpus in that limb. This was a subject fully considered by Gray (1944). Specialised locomotory types will be considered in the appropriate part of the systematic account, and these preliminary remarks refer only to a generalised terrestrial quadruped, the primitive type of Haines (1958).

There are two main functions for the limbs, support and propulsion.

Support is in a sense a passive role, for as long as the joints are held steady by the musculature, compression from the ground can be transmitted up the limb skeleton, and a solid rod of bone could suffice as well as a jointed one.

The propulsive effect of the limb was considered by Gray (op.cit. p.109) to be "the sum of its action as a strut and as a lever". The action as a strut he considered to be in part a passive result of weight acting on an inclined limb, and dependent on the amount of weight and degree of inclination, supplemented by the action of the extending joints. The lever action Gray envisages to be the effect of the extrinsic muscles, for instance the gluteus and iliacus acting on the femur, the spinati and latissimus dorsi on the

humerus (see also Smith and Savage, 1956, analysing the action of these muscles).

The action of the intrinsic musculature seems to be regarded by Gray as

principally to hold the joints rigid so that the limb may act as a lever.

This is an unfortunate emphasis for it overlooks the important part that the extension of the joints by the intrinsic musculature may play in propulsion. Sudden extension of the joints is obviously important in a richochetal mammal such as a kangaroo (Muybridge 1957, pl.167) but its importance is also seen in, for instance, the hind limb action of the galloping cat (op.cit. pl.128).

That Gray has underestimated the importance of this action is confirmed by his explanation of the starting position of a human sprinter (Gray 1961).

This crouched position he supposes to be a means of counteracting that component of the couple, exerted on the body by the hip muscles, which would tip the body.

In fact, this component is countered equally well by the upright, but forward leaning, starting position of the long distance runner. The sprinter's start position enables him to use the extension of the knee and hip joints to provide rapid acceleration.

This point is emphasised here because it is of fundamental importance in understanding the functional differences between the fore and hind limbs, and therefore also the carpus and tarsus.

THE LIMB CYCLE

Haines (1958) briefly considers the phases of limb action in a terrestrial quadrupedal mammal and gives a diagram showing the positions of the skeletal elements; Ottaway considers the limb cycle in more detail, and his account (Ottaway, 1961) will be followed here.

The limb cycle has two main phases, each divided into three overlapping sub-phases. Phases of contact, when the foot is grounded and the body moving forward over it (limb retraction) alternate with periods of recovery, when the limb is off the ground and swinging forward (protraction) for the next contact. The phase of recovery is divided by Ottaway into sub-phases of limb flexion, forward swinging, and then limb extension. During this period of activity, as shown quite clearly by Ottaway's photographs (reproduced as diag. 2, p. 16), the carpus fulfills its role of a flexion-extension hinge, serving to lift the foot clear of the ground, and also to reduce the inertia of the limb by concentrating its mass proximally. The phase of contact is divided into periods of attenuating concussion, weight bearing, and propulsion. During the whole of this time, the wrist is fully in extension, since it is extended before the foot contacts the ground; obviously, some movement must occur between the foot on the ground and the rest of the limb moving with the body over it, but this movement occurs at the metacarpo-phalangeal joint, not at the wrist.

This lack of movement at the carpus during the contact phase is most evident in the long-limbed ungulates, where hyperextension of the carpus would cause excessive lowering of the shoulder. Hildebrand (1961) points out the need for some apparent shortening of the limb between first contact and the vertical position to avoid excessive rising and lowering of the shoulders, but notes that in ungulates this occurs at the fetlock (metacarpophalangeal joint). In Equidae and Ruminatia, in particular, hyperextension at the carpus is not possible, as it is prevented by locking facets (see later, p.23 and Gifford et.al. 1944). This inflexibility contrasts with the

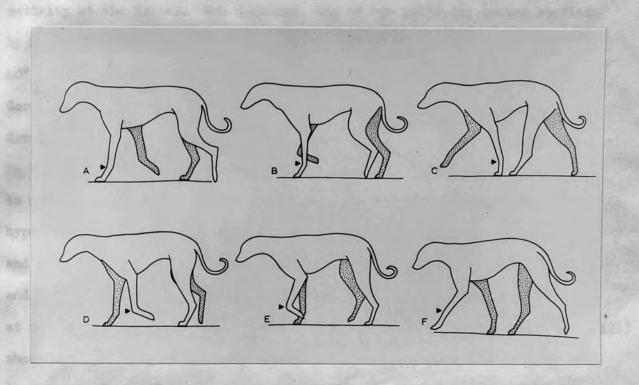


Fig. 2 Phases of action of the (left) fore limb (based on Ottaway, 1961).

The position of the carpus is arrowed.

A-C Phase of Retraction (or Contact).

- A Attenuating concussion.
- B Maximum weight bearing.
- C Propulsion.

During these three sub-phases, the carpus is held constantly in full extension (in fact, in slight hyperextension).

- D-F Phases of Protraction (or Recovery).
 - D Flexing.
 - E Swinging forward.
 - F Extending.

During these three sub-phases, while the foot is off the ground, the carpus is active as a flexion hinge.

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activity at the tarsus. For instance, one of the galloping horses studied by Muybridge (1957, pl.69) shows dorsiflexion of the tarsus increasing from 40° at first contact to 70°, and then the joint extending to about 30° dorsiflexion until the foot leaves the ground. Thus the joint first dorsiflexes to attenuate concussion, then extends to provide propulsion. In the Carnivora, the contrast in function between the carpus and tarsus is not quite so clear. As Hildebrand (op.cit.) shows for the cheetah, some hyperextension of the carpus does occur when the animal is moving at speed and this is also apparent from the photographs in Muybridge (1957, pl.121 and pl.126) for the dog and cat galloping. Even here, the range of movement at the tarsus is much greater than at the carpus. Thus the dog (op.cit. pl.121) shows straightening of the carpus from 40° to 50° hyperextension, while the tarsus goes from 40° hyperextension to 100° hyperextension, then straightens out to only 10° hyperextension.

This difference between the carpus and tarsus applies also to the elbow and knee joints, though less clearly. Hildebrand (1959) describes how the shoulders of the galloping horse rise over the rather rigid fore-limbs while these are on the ground, this despite the hyperextension of the fetlock and the vertical movement of the scapula past the body. This must imply that the elbow is kept in the same degree of extension during the sub-phases of attenuating concussion and weight bearing. Some of the photographic series in Muybridge (1957, especially the camel, pl. 107 and deer, pl.153) suggest that some extension of the elbow occurs during the propulsive sub-phase, and this may apply to the horse. There is not, however, the flexion (or dorsiflexion) then extension, which occurs at the knee, as at the ankle.

In the carnivores, the effect is even more marked, for, as Hildebrand shows for the cheetah, the shoulders continue to fall the whole time that the fore limbs are on the ground. This is corroborated by Muybridge's photographs of the dog and cat. The data given by Manter (1938) do indicate some flexion and extension of the elbow, which would contrast with the present interpretation. However, this analysis concerns a cat walking very slowly, about $2\frac{1}{2}$ m.p.h.. At such slow speeds, balance is a more important consideration than propulsion, and the activity of the elbow is probably directed to maintaining stability. At speed, stability is maintained largely by kinetic energy, and propulsion is more important.

This distinction between the actions of the fore and hind limbs depends on the principles of lever and extending joint actions already discussed. The hind limbs, being behind the centre of gravity, are well sited to provide propulsion by joint extension. The fore limbs, on the other hand, are better placed to produce deceleration than acceleration by this means, but they can provide some propulsion when used as levers. Indeed, Hildebrand demonstrates that, in the cheetah, the body is accelerated past the grounded fore limbs by the extrinsic limb musculature. The use of the fore limb as a lever in this fashion requires that it should be rigid, and there is certainly a tendency towards a rigid lever from the elbow to the fetlock, if not from the shoulder down. The hind limb joints, by contrast, are definitely used at both knee and ankle for propulsion. The heel of the calcaneum provides a powerful lever activated by the gastrocnemius-soleus group of muscles. This lever system at the tarsus in mammals has been investigated many times, from Gregory's (1912) important analysis to Hall-Craggs' (1965) most recent, and Schaeffer

(1947) regards this activity at the tarsus as the functional cause behind the evolution of the double-trochleated astragalus of the Artiodactyla. There is no comparable lever at the carpus; the nearest equivalent might be the pisiform, but apart from the fact that it only takes a fraction of the relevant musculature, it is most ineffectively placed in a hyperextended limb to provide a propulsive lever. It seems very likely that the hyperextension and straightening of the carmivore carpus described above is not controlled by the muscles but is due to the flexor ligaments being overstretched and recovering. If so, the system is comparable to that acting at the fetlock of the horse described by Camp and Smith (1942).

It was mentioned above that the forelimbs are ill-placed to use the extending joint action for propulsion. It is perhaps interesting to note that the vampire bat <u>Desmodus rotundus</u> does in fact use this action when on the ground, but to produce a backwards jump which would serve to carry it away from an awakening victim.

These diverging trends in the fore and hind limbs may well have some basis in ancestral requirements. As the limbs were brought from the laterally directed position of the reptilian ancestors to the position vertically below the body of a mammal, so the requirements for the carpal and tarsal joints to act as flexion-extension hinges must have intensified. The basic requirement at the carpus is a hinge working from 45° to 90° hyperextension, after which the hand can rise over the metacarpo-phalageal joint without causing deceleration of the body (diag. 3, p. 20). At the tarsus, however, the requirement is from 90° to 135° hyperextension. This latter requirement can only be met by the evolution of a pulley sitting on the rest of the tarsus

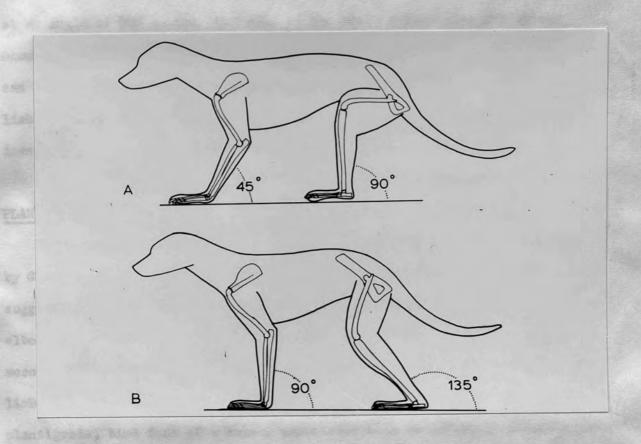


Fig. 3 Requirement for angular movement at the carpus compared with that at the tarsus.

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B Limbs retracted.

at an angle of 90° to the long axis of the foot, a condition met by the mammalian astragalus. The requirement at the carpus is less severe, and can largely be met by the metacarpo-phalangeal joint. The use of the hind limb for propulsion by the extending joint action, the fore limb as a lever, would have reinforced this initial divergence.

PLANTIGRADISM

These considerations lead to a different explanation from that given by Gray (1944) for the evolution of digitgrade from plantigrade limbs. His suggestion is that the plantigrade habit is associated with a bent knee and elbow position, and that the digitgrade stance reduces the tension in the muscles across these joints. In fact, there is no reason why a plantigrade limb must be associated with a bent limb, and consideration of the, classically plantigrade, hind foot of a human, associated with an extremely straight knee, emphasises this point. Equally the knee of a bear appears to be held about as straight as that of a dog. In fact, the majority of plantigrade mammals are small, and with them, a bent limb position is normal. Smith and Savage (1956) have pointed out that, for small mammals, a bounding gait is more efficient than stepping, since the majority of the work done in this form of locomotion is due to lifting the animal's mass against gravity. As already indicated, the extending joint action of the hind limb is well suited to providing propulsion for a bounding gait, hence the frequent association of a bent knee with the bent ankle that is the plantigrade position; unbending both provides propulsion. The digitgrade limb position is essentially a means of elongating the limb for use as a lever, that is for stepping, particularly

in larger mammals where a stepping, rather than a bounding, gait is more efficient (Smith and 'Savage, 1956). The unguligrade position is merely an extension of this lever which can be adopted by forms which do not require to use their ungual phalanges as claws. Thus Carnivora are generally digitigrade Artiodactyla and Perissodactyla are generally unguligrade; but the Chalickotheriidae (Perissodactyla) and Agriochoeridae (Artiodactyla), forms with enlarged claws, were digitigrade.

Having pointed out that the forelimb is most useful as a lever, it is not surprising to note that most of those forms generally termed plantigrade - bear, baboon, hedgehog, etc. - have digit grade fore feet. They may indeed have plantigrade hind feet, but this condition in larger mammals can usually be related to special conditions. In man, for example, it obviously gives better balance, and in the baboon is probably associated with the retention of some climbing ability. The Ursidae do not require speed, since they do not run down their prey in the manner of Canidae or Felidae, but they are of large size; it is probable that their plantigrade hind foot gives better traction and serves to relieve tension in the ankle muscles. (This is contrary to Gray's (1944) opinion that the digit grade stance would relieve tension in these muscles, but is more logical, as anyone trying to stand on tip-toe would agree).

DUAL FUNCTION OF THE CARPUS

From the consideration of the fore-limb function, it is evident that the carpal bones have a dual function, transmitting compressional forces while the limb is on the ground during retraction and providing a hinge joint

during protraction.

Transmitting compression is a passive action for the joints and requires little specialisation; the provision good areas of contact between the bones, and firm ligaments to hold the bones in place, especially on the flexor surface, will suffice. Maintenance of the wrist in the extended position while the forearm is used as a lever is an extension of the same function, and likewise depends largely on the flexor ligaments, with perhaps the flexor musculature. Where a wide range of movement at the carpus is required, no further adaptation for these functions is possible, but where deviation is not required, as the ungulates, the development of "stop-facets" or "locking facets" along the extensor margin of the carpus may occur (fig.4, p.24).

In its function as a hinge, the carpal region may be regarded as essentially two joints closely adjoining. There is a proximal joint (radiocarpal joint) between the bones of the forearm and the proximal row of bones (scaphoid, lunar, and cuneiform); and a mid-carpal joint, between the bones of the proximal row and those of the distal row (trapezium, trapezoid, magnum and unciform). There is a third distal carpal (carpo-metacarpal) joint, but in most mammals very little movement occurs there. The main muscles acting on the wrist extensad are the extensores carpi radialis and carpi ulnaris, which insert on to the bases of metacarpals 2 and 3, and 5, respectively, and the extensor digitorum communis running to the ungual phalanges. Flexad, the flexor carpi radialis runs like the equivalent extensor to the heads of the metacarpals 2 and 3, while the flexor carpi ulnaris runs via the pisiform to metacarpal 5, or to the unciform and metacarpal 5. There are additionally the flexores digitorum (sublimits and profundus) running to the

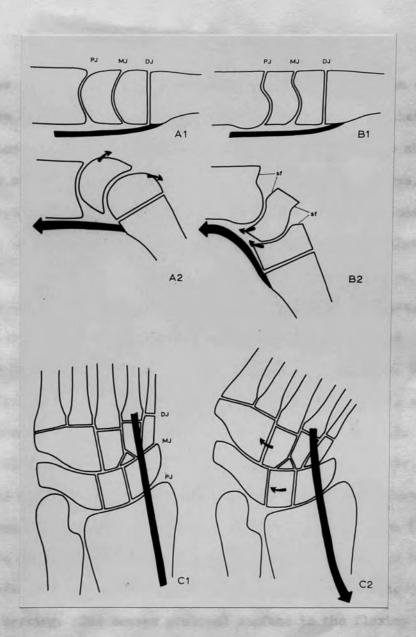


Fig. 4 Basic action of carpal joints, shown on diagrammatic sections.

Al. A2. Proximal surface of each joint concave.

Bl. B2. Proximal surface of each joint convex.

Al. Bl. Carpus extended.

A2. B2. Carpus flexed.

In A, the carpal bones move extensad (i.e. to the extensor, dorsal, surface). In B, they move flexad.

Cl, and C2 show the action in radial deviation. Tension in the muscles of the radial side causes the bones to move to the ulnar side on the concave surfaces forming the proximal side of each joint.

DJ, Distal joint; MJ, Mid-carpal Joint; PJ, Proximal joint; sf, Stop Facet.

phalanges. Since the pisiform is not bound to the cuneiform or the ulna, all these muscles act distally to the two main carpal hinges, so that the detailed direction of movement at the wrist depends largely on the shapes of the articular surfaces of the bones. The ligaments at the carpus, though important for restraining the movements, do not affect the directions of movements except in as far as they hold some bones together and allow others to part.

Movement at the carpus can be reduced, then, to two basic types, depending on whether the proximal surface is convex or concave. As indicated by the diagrammatic sections (fig.4, p.24), if a proximal bone has a concave distal surface, a convex bone surface will adjoin it, and a pull on a flexor muscle distally will cause the second bone to slide extensad on the first, hence flexing the wrist (fig.4a). Conversely, if the proximal bone has a convex distal surface, with a concave surface adjoining it, then the distal bone will move flexad to give flexion (fig.4b). Similar arguments apply to movements in a deviational plane, though here the proximal surface is generally concave, this being a more stable joint form for weight bearing. The convex proximal surface in the flexion plane (fig.4b) is only feasible when accompanied by the development of stopfacets; and stop-facets in the deviational plane would interfere with flexion as well as deviation.

LIMB POSITION

One other important fact related to the functioning of the carpus must be discussed, the position of the limbs beneath the body. The idea of the mammalian limb evolving from a sprawling reptilian position to one with the limbs vertically below the body is well known. The limbs should then swing solely in the fore and aft plane, and simple hinge joints at the carpus, as at the elbow and knee, should be sufficient. If this were the case, it would be difficult to explain why the proximal row of bones, particularly in ungulates, (which do not use deviation at the carpus) should not have a simple cylindrical surface, instead of the complicated arrangement with three separate bones.

The explanation lies in the fact that the therian limbs are not just carried vertically below the body, but are bent medially so as to be brought in under it. This can be quite clearly seen in many of the head-on and tail-on photographic series in Muybridge (1957, especially pl. 68). It is also quite clear to anyone who has followed, for instance, fox (Vulpes vulpes) tracks in snow, for the prints of the feet lie all on a straight line (see photo. in Leutscher 1960). Bringing the feet under the body in this manner must serve to reduce the yawing which would be produced by a single limb acting to one or the other side of the mid line, or to reduce the lateral toppling which support from a pair of limbs (one fore with one hind) might cause. The importance of this factor can be seen in a contrary way in the gait of a hedgehog (Erinaceus europaeus); here the limbs are too short to be brought under the body, and the body rolls from side to side during locomotion to compensate. The rolling gait of a sailor is a similar case. In man the feet are usually placed almost on a straight line, but a sailor has to counteract the roll of a ship. To do this, he walks habitually placing his feet somewhat out to the side, and on land must sway his body from side

to side, to keep it over the grounded limb. Ottaway (1956) mentions a slight roll in a slow-moving dog as a possible counter to lateral thrusts.

In the forelimb, this medial bending of the limb is largely achieved at the elbow. At the carpus the limb is bent laterally, bringing the long axis of the manus (as seen from anteriorly) back perpendicular to the ground. This presumably keeps the foot level on the ground. The medial bending at the elbow is therefore about equalled by the lateral bending at the wrist. The bending is greater in wide bodied and short limbed mammals than in slim bodied or long legged forms, as would be expected if the limbs were to be placed proportionately as far under the body in each case. In Rhinoceros and Hippopotamus the angle as seen from anteriorly between the long axes of the humerus and radius is about 20°, in a roe deer (Capreolus) it is only 6°.

The effect of this inbending of the limbs is to require that the feet swing outwards round one another in the recovery phase. In the forelimb this is done from the elbow, which flexes obliquely and carries the forearm laterally (fig. 5, p. 30). Due to the original configuration of the elbow joint (the radius articulating on a condyle while the ulna slides in a groove) this elbow flexion follows a spiral course causing semi-supination. In other words, when the elbow is flexed the flexor surface of the manus faces medially across the animal. Straight flexion at the carpus from this position would throw the hand across the body to hit the other fore limb. In fact, carpal flexion is not "straight" either, but carries with it some ulnar deviation which tucks the manus ventral to the semi-supinated forearm.

This ulnar deviation is apparent in most mammals; indeed, Johnston (1907)

noted its occurrence in the human hand. It is however most important in the long-limbed ungulates. The precise method by which it is achieved varies between different animals, and a detailed consideration of these methods is included where appropriate in the systematic survey. However, the methods used fall into three general groups which may be considered here.

- In its simplest case, the occurrence of ulnar deviation with flexion is, like the spiral action of elbow when flexed, an accident of the primitive (carpal) configuration. The scaphoid and lunar are convex proximally, sliding in the concavity of the distal surface of the radius, so move extensad in flexion (compare fig. 3a and b., p.20).

 Conversely, the cuneiform is concave proximally, and in flexion slides flexad round the convex styloid process of the ulna. This rather oblique joint action is sufficient to cause ulnar deviation (fig.6a,p.31).
- 2) In some mammals, either the proximal joint or the mid-carpal joint is curved in the transverse, (radiad to ulnad) plane, giving a joint at which deviation can be produced (fig. 32,p.20). If this surface is more sharply curved toward the ulnar side than on the radial side, pressure from the flexor muscles will push the steeper curve into the deeper part of the concavity opposing it, again causing ulnar deviation. This is what happens in the human wrist, and it can be countered by the deliberate action of the muscles which normally cause radial deviation. In other animals the prestence of a flexad-projecting tubercle on the scaphoid may hinder the flexion of the radial side of

the carpus while allowing the ulnar side to flex and move radiad - this is the situation in carnivores and various other groups (fig. 6b).

In the ungulate groups, the carpus is developed as a specialised flexion hinge, and the carpal bones move flexad at both joints. The surface over which the bones on the radial side flex is, however, a larger surface (i.e. a curve of greater radius) so that these bones move further in a flexad direction than those on the ulnar side. If the bones of (usually) the proximal row move as approximately one unit ("approximately" because some adjustment between adjacent bones is unavoidable) then the joint is oblique, rather as in case 1 above, and gives ulnar deviation. In certain cases, the bones of the proximal row move past one another, and do not themselves give the ulnar deviation, but provide, in the flexad position, an uneven surface on which the distal row must flex. The principle is the same, but the ulnar deviation arises at the midcarpal joint rather than the proximal joint(fig.6b).

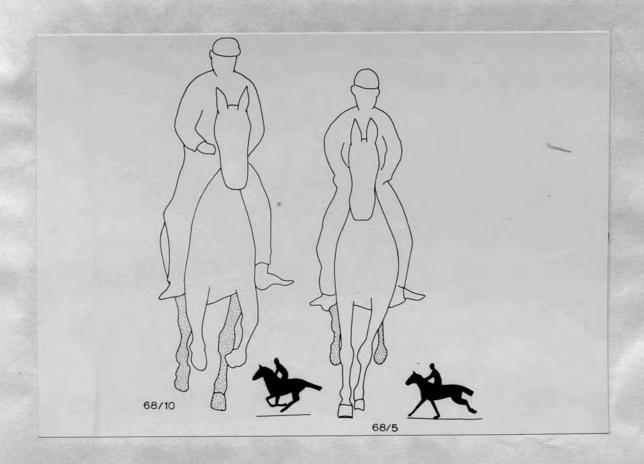


Fig. 5 Positions of the fore limbs of a horse as seen from head-on. Drawn from Muybridge, 1957, plate 68. In frame 10, the fore limbs are off the ground, protracting, and passing one another (silhouette); seen head-on, the carpi are far apart. In frame 5, one fore limb is grounded, the other almost so; seen head-on, the carpi are close together, almost one behind the other.

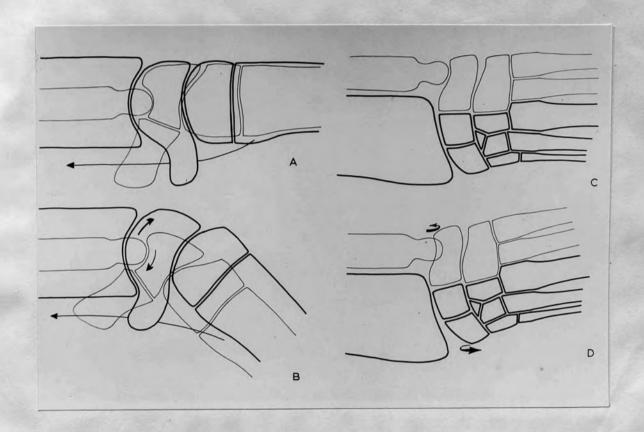


Fig. 6 The combination of ulnar deviation with flexion.

- A-D in the basic mammalian wrist.
 - A from the radial side, wrist extended.
 - B from the radial side, wrist flexed.
 - C from the extensor side, wrist extended.
 - D from the extensor side, wrist flexed.

The radial side of the carpus is drawn in heavy lines. The radius is concave distally, hence the scaphoid slides extensad in flexion (B); the ulna is convex distally, and the cuneiform slides flexad round it (B), (cf. Fig 4, A2, B2) and also somewhat proximally (D.).

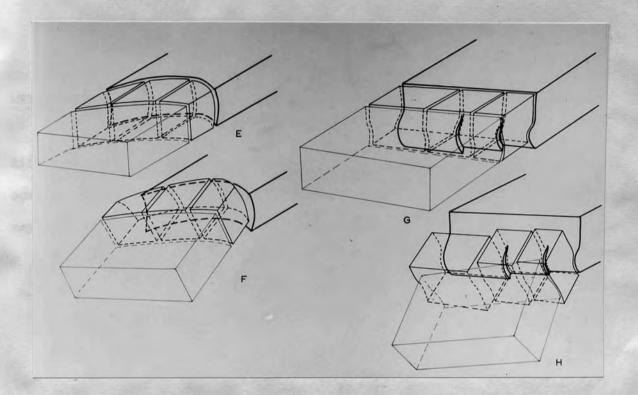


Fig. 6 (Continued)

E-F diagram of the condition in e.g. primates.

E in extension.

F in flexion.

The whole of the proximal row articulates with the radius (heavy lines) which is more steeply curved on the ulnar than on the radial side. The proximal row of bones moves away to the radial side in flexion.

G-H diagram of the condition in ungulates.

G in extension.

H in flexion.

The distal surface of the radius (heavy lines) in "stepped", the curvature on the ulnar side being greater (i.e. the radius of curvature is less). The bones of the proximal row, flex round these surfaces, but in doing so make an uneven, slanted surface for the more distal bone(s) (thin lines).

SECTION II

SYSTEMATIC SURVEY

METHODS AND MATERIALS

A number of procedures have been used to investigate the carpi of different mammals, their use depending on the nature and availability of specimens, and on the usefulness of the methods. Five principal methods may be enumerated:-

- 1. Johnston's method
 - 2. Embedding pins
- 3. X-radiography diameter to mental the between these
- 4. Serial sectioning post tions, (flexes, in
- 5. Manipulation the design of the resultant
- 1) Johnston (1907) investigated the human carpus by fixing dead material in a predetermined position, dissecting out the carpus from one side, and making a cast of the exposed bone surface. The process was then repeated from the other side, to give two casts in which the now clean bones could be placed.

This method is only practicable for larger mammals (fox or badger upwards) and requires several specimens of each, one to fix in a flexed position, one extended etc., It has advantages (a) that all the bone surfaces can be checked and (b) that a permanent record is obtained, since the bones can be removed from and replaced in the casts.

2) Wright (1935) and others have used pins embedded in the carpal bones to investigate the human carpus. As an extension of their method, a long pin was embedded in each bone and the carpus illuminated from one side. The shadows of the pins move through the appropriate angles when the wrist is flexed, giving a measure of the amount of flexion of each bone.

This method also is limited to large animals, and has the more serious limitation that it can only measure (angular) movement in the flexion-extension plane. It provides, however, a useful check on other methods, and has the advantage that the carpus is little disturbed by embedding the pins.

X-rays provide a method somewhat intermediate in results between these two. By fixing the wrist in various desired positions, (flexed, in radial deviation, etc.), and superimposing the images of the resultant radiographs, the angles of movement of the various bones can be measured.

is explained seption, the carpal bones are moved by masoles sorting

The method remains useful for animals of smaller size than the others, but has the particular limitation that the shadows of the bones in radiographs taken from radiad (or ulnad) to measure flexion-extension movements overlap considerably. This frequently means that movement can only be measured for the two joints (proximal and mid-carpal) and movements between the bones of one row may not be seen.

4) Serial sectioning is the only comparable method for use on very small material. The specimen is first fixed in the desired position and then

impregnated with celloidin. (The material proved too hard for wax-embedding). Sections have been cut at 20 μ , and stained in haemotoxylin with eosin - Biebrich's scarlet counterstain. As with Johnston's method, this requires several specimens of each animal, and is additionally very time consuming.

- 5) All these methods are subject additionally to the main limitation that the actual movements of the carpal bones cannot be observed. Manipulation of the carpus in some form or other is the only method which overcomes this criticism.
 - a) Manipulation is most satisfactory when applied to fresh dead material. As explained earlier, the carpal bones are moved by muscles acting distally to the carpal joints, so that the movements can be reasonably mimicked by manipulation, so long as care is taken not to overstrain the ligaments and tendons. By repeating the manipulation after the removal of successive layers from the extensor surface, first skin, then muscles, then ligaments and joint capsule, it is possible to check that the movements produced are still realistic; while after the removal of the joint capsule and ligaments, the movements of each bone can be seen. In many cases it has been possible to use embedded pins and X-rays on the specimen before manipulation.
 - b) When skeletal material only has been available, the method used has involved glueing the bones together into functional units, usually forearm, proximal row, distal row and metacarpus, and moving these units on one another. The glue used was Copydex, a rubberoid glue which can readily be peeled off, allowing different combinations of bones to be

studied. This type of material is obviously less easy and reliable to interpret than fresh dead limbs.

c) In some cases, skeletal material with the ligaments still in place has been available. Soaking these in water softens the ligaments (even in 100 year old specimens) sufficiently to allow movement, though probably never as freely as in life. In the absence of other material, this has provided some check on results obtained from clean skeletons.

In the main, the descriptions of the movements which follow are based on manipulative studies, and the nature of the material available for these is indicated. Supplementary information for some mammals was obtained as follows;

- 1) Johnston's method: Vulpes, Meles, Ovis, Sus.
- 2) Embedding pins :- Canis, Galera, Ovis, Capreolus, Equus, Papio, Myocastor,

 Castor, Macropus; also, from a preserved specimen,

 Zalophus.
- X-ray photographs have been obtained from fresh dead specimens of:Vulpes, Meles, Galera, Capreolus, Equus, Mandrillus,
 Tamandua, Sciurus, Castor, Lepus, Erinaceus, Pteropus
 and Macropus; also from preserved specimens of
 Zalophus and Phascolomys, and softened ligamentary
 specimens of Ateles and Choloepus.
- 4) Serial sections have been cut of the hands of:
 Cavia, Rattus, Sorex, and Talpa. Those of Sorex

show the wrist in ulnar and radial deviation, flexion and extension, while two series of sections of Talpa show extension and hyperextension. For the other two genera, only series of sections to show the form of the carpal bones in radio-ulnar section and flexor-extensor section have been prepared (see p.38).

For recording movements obtained from manipulation rough measurements have been taken with a protractor. Deviation has been measured between the long axes of the radius and metacarpal three. Flexion or extension has been measured between the extensor surfaces, as seen from the side (from radiad or ulnad), of the radius and metacarpal three.

Wright (1935) is highly critical of such inaccurate or inexact methods, and advocates exact measurement of angular movement, and specification of the axes of rotation. While accurate measurement of angular movement may be possible from radiographs, it is not feasible from solid material.

Moreover, exact measurements are rarely repeatable, since the angular movements produced vary considerably, both between individuals, and with successive movements of one individual. As an example, Wright gives the total measurement of flexion-extension in the human carpus, from radiographs, as 130°, while the radiographs in Gray's Anatomy (Johnston, T.B. et.al. 1958) give 117°. A difference of 13° is not in itself a large discrepancy, but does nullify any attempted accuracy. Any attempt to define axes of rotation is even less valid, for such an axis will only exist if a bone surface is cylindrical. Frequently, the surface is one of increasing curvature (in which case the "axis" is in fact a plane, not a spindle) or may be two surfaces

curving in two opposite directions. Furthermore, as already indicated,
flexion is not confined to the flexor-extensor plane, but invariably
includes some ulnar deviation.

No attempt has been made to indicate axes of rotation therefore, but considerable attention has been devoted to the shapes of the articular surfaces. Diagrammatic sectional drawings have been made to aid the description and understanding of these features. These have been drawn in flexor-extensor and radio-ulnar planes, to illustrate the surfaces operative in flexion and deviation respectively. For convenience, these will be referred to as FES (flexor-extensor sections) and RUS (radio-ulnar sections).

In addition to these sectional diagrams, there are drawings of the proximal and distal surfaces at each joint. These have been drawn alternately as mirror images, or as though from left and right wrists - thus the right radius and ulna is drawn above the left scaphoid, lunar and cuneiform. The radial side of all the bones is therefore on the same side of the diagrams, and the opposing joint surfaces can be directly compared. This is comparable with the drawings of left maxillary with right mandibular tooth rows used by dental anatomists to illustrate occlusal relationships.

Where possible, the results obtained from these post-mortem methods have been checked, for over-all mobility of the wrist, by reference to cine film and the photographic series in Muybridge (1957). From the preceding comments on methods used, it is obvious that the most useful material has been fresh dead (or frozen) limb specimens. For less common animals, only skeletal material has been available, mostly specimens in the osteological collections of the British Museum (Natural History). The few fossil carpi that have been examined are also from the British Museum collections. The relevant museum

collection numbers, prefixed B.M. (N.H.), are given when material is listed.

5. Distal surface, foreers booss.) Proximal derpal 6 Frozinal surface of proximal carpal row) joint 7 Distal surface of proximal corpal row) Nid parpal S Province surface of distal carpal row) joint 9 Distal surface of distal carpal row ...) Distal carpal Pi Piatforn some and the same thing the second of the same to the same than the same t Dashed liess and numerals 1---1, 2---2, etc. on the drawings

of surface views indicate the planes of sections, diagrams 1,2, sto.

KEY TO DIAGRAMS

1.	Radio-ulnar section		
2-4	Flexor-extensor sections		
5	Distal surface, forearm bones	Proximal carpal	
6	Proximal surface of proximal carpal row	joint	
7	Distal surface of proximal carpal row	Mid carpal	
8	Proximal surface of distal carpal row	joint	
9	Distal surface of distal carpal row	Distal carpal	
10	Proximal surface of metacarpus	joint	
Ce	Centrale (fig. 7, p. 45) or fox may be considered as an example		
Cu	Cuneiform paryone, and one that has been studied by most of the		
Lu	Lunar		
Mc 1-5	Metacarpals 1 - 5		
Mg	Magnum a field scaphoid, huser, and contrate of the printity		
Pi	Pisiform 1871, Matthew 1905 h. The Land In 1905, this bone		
Resoth	Radius personal surface which fits neatly into the community		
Sc	Scaphoid our caree is centinged wheat by the proximal surface		
ScL	Scapholunar and the this plans presents a ratherest		
Td	Trapezoid Tanger monvity in the southolesse for the eaging		
Tm	Trapezium eraperoid, and an angular surface for the undiform		
Un	Unciform was someholusar, on the other by the cunciform		
U. 200	Ulna lowion place, the surfaces are generally a occopying on		
Dashed lines and numerals 11, 22, etc. on the drawings			
of surface views indicate the planes of sections, diagrams 1,2, etc.			

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CARNIVORA - FISSIPEDIA

The carpus of the Carnivora is considered first, not because it represents some central type, but because it provides an introduction to working of the carpus in both flexion and deviation.

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CANIDAE

Material:-

Cenis Familiaris - dog - fresh dead and skeletal.

Vulpes vulpes - fox - fresh dead and skeletal.

The carpus of a dog (fig. 7, p. 45) or fox may be considered as an example of a typical Carnivore carpus, and one that has been studied by most of the available methods.

The most distinctive feature of the Carnivore carpus is the scapholunar bone, representing the fused scaphoid, lunar, and centrale of the primitive mammalian carpus (Flower 1871, Matthew 1909). As seen in RUS, this bone has a smooth convex proximal surface which fits neatly into the concavity of the radius; this convex curve is continued ulnad by the proximal surface of the cuneiform. The mid-carpal joint in this plane presents a rather irregular surface, with a deep concavity in the scapholunar for the magnum, a shallower one for the trapezoid, and an angular surface for the unciform provided on one side by the scapholunar, on the other by the cuneiform.

In FES, the flexion plane, the surfaces are generally a concavity on the proximal side of the joint, and a convex bone fitting in to it. The scapholunar has a more complicated shape, however. At the radio-flexad corner, the bone is developed into a large tuberosity. The base of this tuberosity fits over the flexad margin of the distal surface of the radius; in FES, therefore, the proximal surface of the scapholumar appears S-shaped. The distal end of the ulna is a convex, condyloid surface, but the cuneiform is little hollowed to receive it; rather the ulna overlaps distally past the cuneiform on its ulnar side.

The bones of the distal row are tightly bound together by ligaments and move as one unit. The metacarpals similarly act as one unit, though they are able to flex slightly ($\langle 10^{\circ} \rangle$) past one another. The scapholunar and cuneiform are also quite tightly bound together, but are able to rock somewhat on one another such that their distal surfaces tend to face each other; the movement is essentially adduction.

Deviational movements occur solely at the proximal joint, the mid-carpal joint being much too irregular in this plane (fig. 8, p. 46). The range of movement is about 20°, from 5° radial deviation to 15° ulnar. The movement is achieved by the scapholunar and cuneiform sliding ulnad or radiad on the radius.

Flexion movements are more complicated, and involve both proximal and mid-carpal joints. The total range of flexion-extension movements is about 160°. Some slight movement, less than 10° of flexion, may occur between the metacarpals and the distal row, about 35° at the mid-carpal joint, and the rest of the movement at the proximal joint. At the mid-carpal joint, the dominant feature is the joint between the scapholunar and the magnum. The scapholunar bears a groove on its distal surface in which the wheel-like proximal surface of the magnum slides. This groove is oblique,

about 10° from the flexion-extension plane (nearer the radial side flexed, the ulnar side extensad) but the opposing surface of the magnum is similarly inclined. Thus when the magnum slides extensad up the groove during flexion, the magnum, and the distal row as a whole, move somewhat ulnad, but the flexion movement is straight, that is, restricted to the flexor- extensor plane. The movement in fact is analogous to that produced by lifting hinges sometimes fitted to doors; the door moves in a straight, closing direction (no twisting) but moves upwards at the same time. The unciform has a proximal surface which is almost as curved as that of the magnum, and thus slides on the scapholunar with the magnum. This facet of the unciform however, is lifted off the scapholunar by the ulnad movement. The trapezoid is a rather flat bone, shallow in its proximal-distal dimension, and in flexion is completely out of centact with the scapholunar, though the trapezium (which lies flexad, below, rather than radiad, beside, the trapezoid) remains in contact. The flexion movement at the mid-carpal joint is limited by the heel of metacarpal 5 meeting the unciform and by a stop facet on the flexor surface of the unciform which meets the scapholunar. The reason for the oblique movement of the distal row in flexion is seen when the reverse movement, extension, is considered, for this brings the out-of-contact surfaces into contact as stop-facets, locking the joint in the extended position. The locking so produced is better than it could be if the midcarpal flexion were straight, for that would require undercutting the articular facets to provide room for the bones in the flexed position.

Flexion at the proximal joint is complicated by the concurrence of

ulnar deviation. The tubercle of the scaphoid is clear of the flexor margin of the radius in the extended position and 20° of flexion occurs before contact is made. For further flexion, the scapholunar has to slide radiad, i.e., giving ulnar deviation. The "styloid process" of the radius, that is, the distally projecting radial margin, is drawn across the groove at the base of the tubercle of the scapholunar, and the cuneiform, sliding with the scapholunar, glides inside, radiad, of the styloid process of the ulna. Because the carpus is flexed, the deviation so produced, 20°, is rather more than can be produced in the extended position. This provides the "ulnar deviation with flexion" alluded to in the introduction (p.27) as necessary if the recovering limb is to pass the grounded one without interfering.

Further flexion of the proximal row on the forearm occurs by the scapholunar rocking on the flexor margin of the radius, and the cuneiform sliding against the ulna on its ulnar side. In the position of full flexion, therefore, the main, convex, weight bearing surfaces of the scapholunar and cuneiform are completely out of cantact with the radius and ulna.

One other movement occurring at the wrist is supination. As in man, this is primarily a movement of the radius on the ulna, and reaches 20°.

All the carpal bones move with the radius, and the twisting movement is between the ulna and cuneiform.

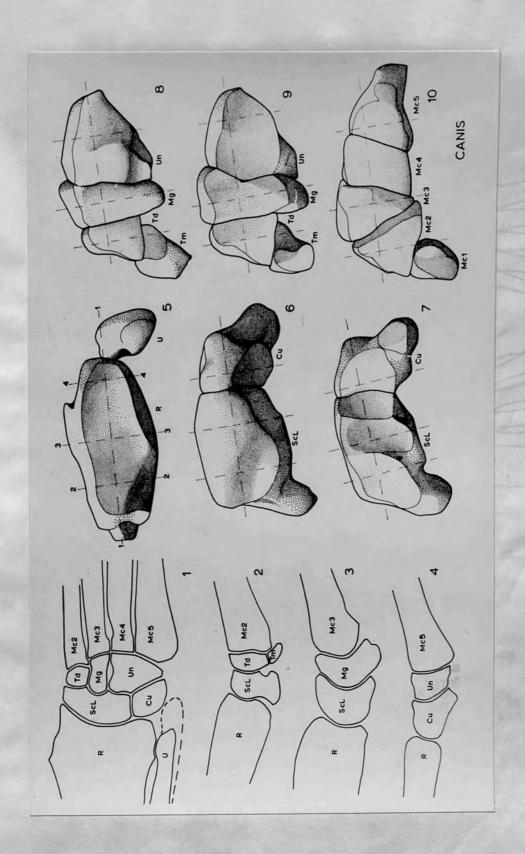


Fig. 7 Carpal diagram of Canis.

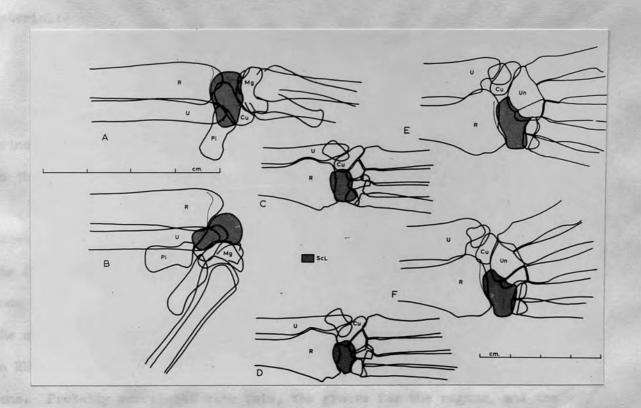


Fig. 8 Action of the carnivore carpus, drawn from radiographs.

A Vulpes, radial view, in extension.

B Vulpes, Radial view, in flexion. The extent to which the body of the scapholunar parts from the radius can be seen.

C Vulpes, extensor view, radial deviation.

D Vulpes, extensor view, ulnar deviation. Less movement is apparent than can occur in life. The cuneiform and scapholunar move together.

E Meles, extensor view, radial deviation.

figite of and plantingade in often stated. This point is comfirm to be

Meles, extensor view, ulnar deviation. The scapholunar and unciform move together, the latter sliding past the cuneiform.

MUSTELIDAE

Material:-

Meles meles - badger - fresh dead

Galera barbara - tayra - fresh dead

The mustelid carpus resembles that of the Canidae both in form and the principal movements that occur. This account will therefore concentrate on the points of difference.

Morphologically, the cuneiform differs in that it is more concave proximally, and articulates more with the distal end of the ulna than with the (radial) side of the styloid process (fig.9, p.48). The unciform is a much wider bone (ulnad - radiad) and has a relatively larger contact with the cuneiform. The distal surface of the scapholunar is much more irregular in RUS, the surfaces for the magnum and unciform being cut deeper into the bone. Probably correlated with this, the groove for the magnum, and the magnum itself, are set more obliquely, 20°, with respect to the flexion-extension plane.

The range of movement is rather less than in the Canidae, in particular, flexion stops at 120°. It seems probable that this is limited by the shortness and stoutness of the forefoot and the crowding of the flexor side of the carpus in the flexed position. Also, with a shorter foot, the extreme of flexion is not necessary to clear the ground during the recovery phase of the limb. In the badger, as the dog, hyperextension is limited to 10° (20° if the ligaments are stretched by pressure), so that the badger is digitgrade, not plantigrade as often stated. This point is confirmed by a comparison of the footprint with that of a dog (see Leutscher, 1960) which

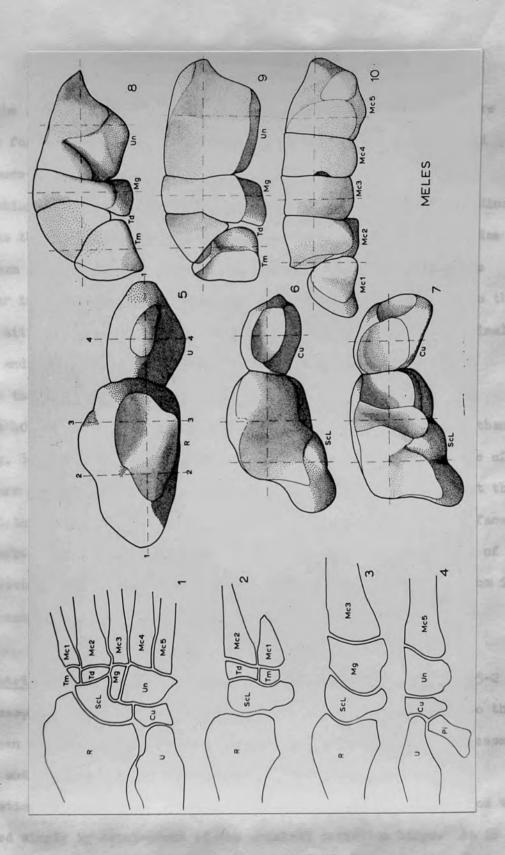


Fig. 9 Carpal diagram of Meles

presents the same pattern of pad-marks. The tayra possesses rather more capability for hyperextension, to at least 30°, which may be correlated with its more arboreal life.

Deviation occurs principally by the scapholunar sliding on the radius, but whereas the cuneiform moves with it in the Camidae, in the Mustelidae the unciform slides across the cuneiform, which is thus parted from the scapholunar in ulnar deviation. This may be explained as partly due to the cuneiform sitting more tightly on the ulna because of its concave proximal surface; and partly due to the wider unciform, which has its proximal surface on the same curvature as has the scapholunar.

About 40° of flexion occurs at the mid-carpal joint, little more than in the dog, despite the greater curvature. The larger proximal surface of the unciform pushes the cuneiform ulnad, away from the scapholunar. At the proximal joint, less movement occurs and the curvature of the rocking facet is less marked. The cuneiform slides flexed round the styloid process of the ulna rather than inside it during flexion, as might be expected from its concave proximal surface.

Enhydra lutris - sea otter - skeletal material only BM(N.H.) 1934-8-5-2

The carpus of the sea otter (fig. 10, p. 50) conforms essentially to the pattern seen in other mustelids, and the only differences concern increased deviation and reduced flexion capabilities.

Deviation seems to range through 40° (20° radial to 20° ulnar), and this is acheived simply by development of the proximal deviation hinge. As in the badger, the cuneiform moves little on the ulna and the unciform slides past

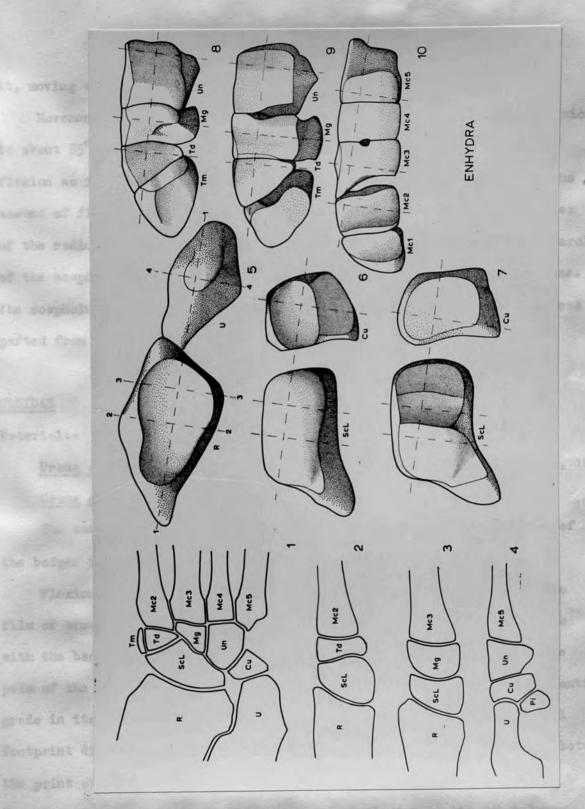


Fig. 10 Carpal diagram of Enhydra

it, moving with the scapholunar.

Movement in the flexion-extension plane occurs from 20° hyperextension to about 85° flexion. The mid-carpal joint provides the same amount of flexion as in other mustelids, 40°, and the reduction is therefore in the amount of flexion occurring at the proximal joint. The opposing surfaces of the radius and scapholunar (as seen in FES) are flatter, and the tubercle of the scapholunar is more on the radial than the flexor side of the bone. The scapholunar thus rocks much less on the radius, and in flexion is less parted from it extensad.

URSIDAE

Material: -

<u>Ursus arctos</u> - brown bear - skeletal material BM(N.H.) 965a, 1010g Ursus arctos ssp. - kodiak bear - fresh dead

The carpus of the bear (fig. 11, p. 52) resembles very closely that of the badger in form and function, and little need be said.

Flexion is limited to 90°, a figure confirmed by analysis of a cine film of brown bear galloping, and 55° of hyperextension is possible. As with the badger, this amount of hyperextension is not sufficient for the palm of the manus to be applied flat to the ground; the bear is not plantigrade in its forefeet. This conclusion, again is supported by the usual footprint diagrams (eg. Brink 1955) which indicate also the difference between the print of the forefoot and that of the truly plantigrade hindfoot. Surprisingly, the hyperextension is caused mostly not by the scapholunar being able to slide further flexad on the radius, but by a change in the

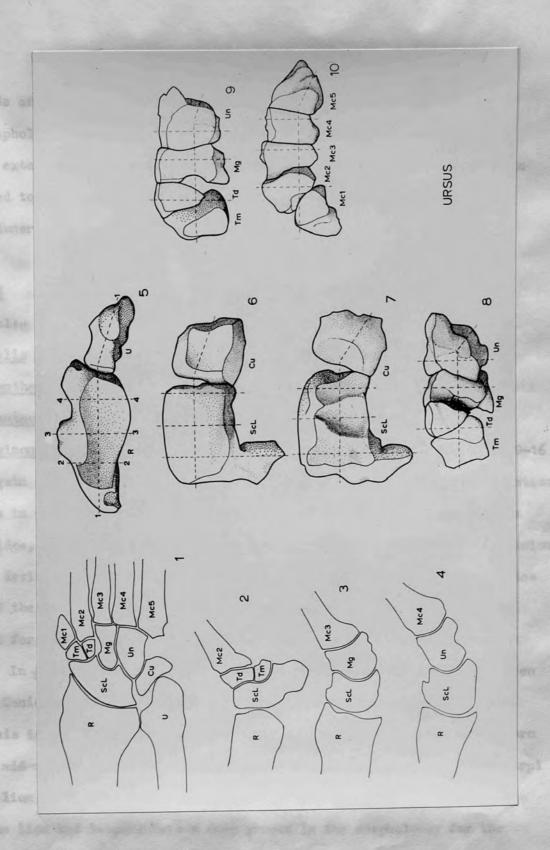


Fig. 11 Carpal diagram of <u>Ursus</u>.

attitude of the distal surfaces. Thus, instead of the distal surface of the scapholunar being diametrically opposite the proximal surface it is tilted extensad. The extensor side of the bone is thus "compressed" when compared to that of, say, a dog, and the distal row of bones sit on the scapholunar in a position of 35° hyperextension.

FELIDAE

Material:- of any are at the sometimes diseased and provided a machanism

Felis catus - domestic cat - fresh dead

Panthera ? leo - ?lion (or tiger) - skeletal

Panthera pardus - leopard - skeletal 1935-9-19-3

Acinonyx jubatus - cheetah - skeletal BM (N.H.) 1940-1-20-16

Again the carpus of the Felidae (fig.12,p.55, and fig.13, p.56) functions much as in other Carnivora. The proximal joint has much the same form as in Canidae, and the same range of movement is possible, about 120° of flexion, 20° of deviation. The mid-carpal joint, at least in the Felinae, resembles that of the Mustelidae and Ursidae, in the scapholunar being more deeply grooved for the magnum etc; about 40° of flexion occurs at the mid-carpal joint. In Acinonyx the mid-carpal joint is of the less irregular type seen in the Canidae, though the amount of flexion occurring is about the same.

This is an appropriate point to consider these differences in the form of the mid-carpal joint, in view of Hopwood's (1947) discussion of the carpi of the lion, leopard and cheetah.

The lion and leopard have a deep groove in the scapholunar for the magnum, a strong ridge across the face for the trapezium and an S-shaped

(in FES) surface for the unciform.

The mid-carpal joint of the Mustelidae and Ursidae has a somewhat similar arrangement, particularly the deep groove for the magnum, features which suggest that the carpus interlocks more effectively at this joint. The cheetah, like the Canidae and also the Hyaenidae (see later) has a rather flatter distal surface to the scapholunar.

Considering particularly the felids, Hopwood considered that the features on the distal surface of the scapholunar diverged and provided a mechanism for spreading the metacarpals and hence the toes. He considered that the lesser development of these features showed the loss of this ability in the cheetah and its mechanical concentration on a straight flexion-extension movement for running.

However, as already indicated, the distal carpal row in carnivores is tightly bound together and acts as one unit. Further, the metacarpals are tightly bound at both proximal and distal ends, and cannot be spread - spreading of the toes occurs from the metacarpo-phalangeal joint. The ridge for the trapezoid is in fact parallel with the groove for the magnum, not divergent, while the surface for the unciform is not in contact in the flexed joint but serves as a lock.

One thing which the forms with the deeply grooved scapholunar have in common is some climbing ability, the other forms are more extreme cursors. Carnivores tend to climb by hugging the tree they are scaling, which must, somewhat unusually, require using the wrist in a somewhat flexed position. It is suggested, therefore, that this grooving of the scapholunar produces a firmer joint, perhaps to resist twisting, for this sort of activity.

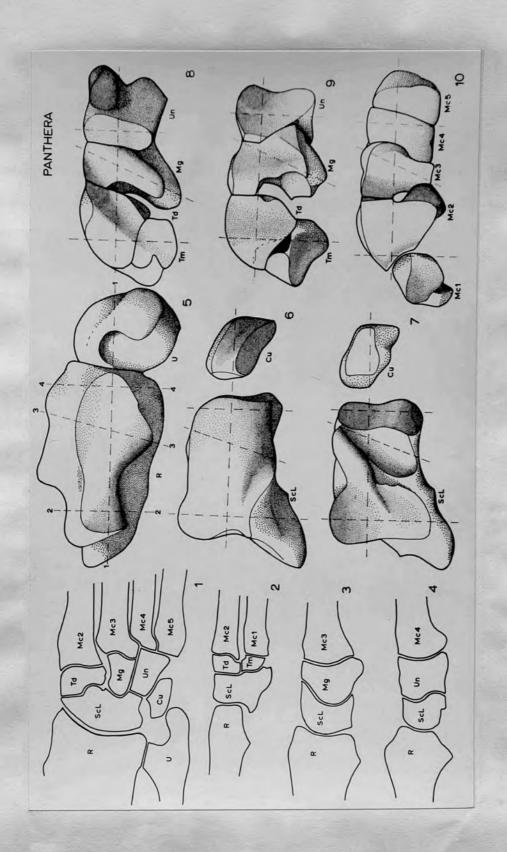


Fig. 12 Carpal diagram of Panthera

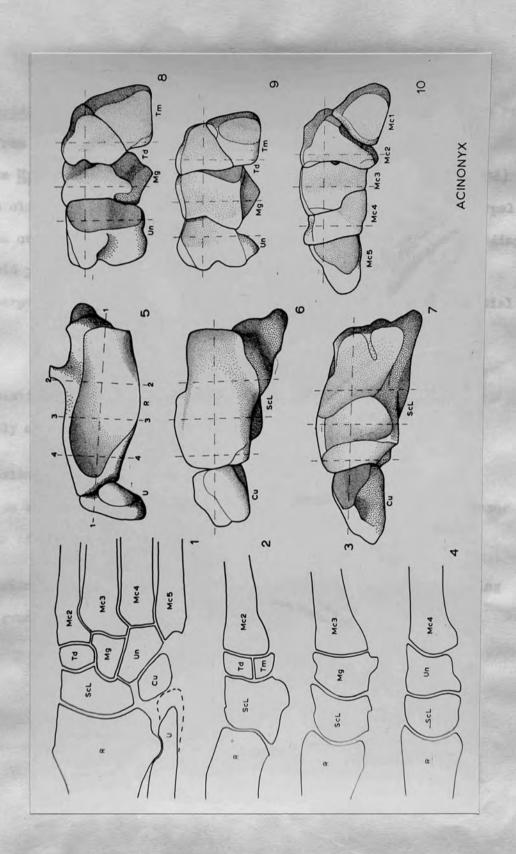


Fig. 13 Carpal diagram of Acinonyx

<u>Viverridae</u> have a carpal arrangement closely resembling that of the Felinae, to judge from the carpus of Viverra civetta (BM(N.H.) 138d).

In the <u>Hyaenidae</u>, (<u>Crocuta crocuta</u>, BM(N.H.) 1934-4-1-137, and 1233d) the carpus closely resembles that of a canid, with a rather flat mid-carpal joint. The cuneiform has, in RUS, a rather flat surface for a correspondingly flat styloid process to the ulna.

The carpus of the Carnivora may be summed-up as having three essential features.

- 1) A deviational hinge at the proximal joint provided by a scapholunar broadly convex, in RUS, sliding on the radius.
- 2) A flexion hinge at the proximal joint, providing most (70%) of the flexion at the carpus, involving the scapholunar rocking on the flexor margin of the carpus.

- lumpard soul - skeletal LM(N.H.) 1959-12-17-4

3) A flexion hinge at the mid-carpal joint centred on the magnum sliding in a groove on the scapholunar.

The curpus of the gray stal (fig.14, p.61.) may be used to describe and

Figure 60, and Packhouse has described how the forearm may be used in a

I wal interpretation is based on the study of the Similar Puna and Phone.

CARNIVORA - PINNIPEDIA

The carpi of the seals and sealions were briefly compared by Howell (1928), and the grey seal was considered further by Backhouse (1961). The pinnipedes have the same bones in the carpus as the fissipedes, including a scapholunar, but present several different functional patterns which are considered separately.

Material:-

Halichoerus grypus - grey seal - skeletal BM(N.H.) 1938-12-1,

1958-11-28-1

Phoca vitulina - common seal - fresh dead

Pusa sibirica - Baikal seal - fresh dead

Ommatophoca rossi - Ross seal - fresh dead

Hydrurga leptonyx - leopard seal - skeletal BM(N.H.) 1959-12-17-4

Zalophus californianus - sea-lion - preserved specimen

Zalophus californianus - seal-lion - skeletal BM(N.H.) 1884-4-15-1

Odobenus rosmarus - walrus - skeletal only BM(N.H.) 1950-10-30-1

HALICHOERUS GRYPUS

The carpus of the grey seal (fig.14, p.61.) may be used to describe an example of the "typical" Phocidae. In form, it diverges less from that of the fissipede, and Backhouse has described how the forearm may be used in a manner closely resembling the action in terrestrial carmivores. The present functional interpretation is based on the study of the similar Pusa and Phoca,

these three genera all being members of the tribe Phocini. The scapholunar presents a rather flatter proximal surface to the radius than in fissipedes, and in particular the tubercle is displaced toward the radial side. The cuneiform is an angular bone which has a facet radiad corresponding to one on the ulnar side of the radius and is deeply hollowed on its ulnar side to receive the styloid process of the ulna. In extension, it is tightly wedged between the radius and ulna. At the mid-carpal joint, the trapezium is much enlarged (commensurate with the large size of the metacarpal 1) and forms a smooth convex proximal surface with the trapezoid in both RUS and FES. The magnum and unciform are less curved in FES, and the magnum does not present a "wheel-shaped" proximal surface but is wedge-shaped in RUS.

The metacarpals are much less tightly bound together than in fissipedes, particularly distally, and can move considerably relative to one another. The proximal ends of metacarpals 4 and 5 are rather rounded in RUS, and metacarpal 5 bears a wedge shaped appearance in FES, due to a flexor facet which articulates on the extensor side of a distally projecting tongue on the cuneiform.

Flexion is the main movement of the proximal joint. The scapholunar slides extensed up the distal surface of the radius and then rocks on the flexor margin, while the cuneiform slides flexed round the styloid process of the ulna, and parts from the radius. This produces 50° of flexion, which is accompanied by 20° ulnar deviation as the radius is "higher", more distally produced, on the radial side. This combination produces the propulsive flick at the end of a paddling stroke described by Backhouse. A further 70° of flexion is produced at the mid-carpal and distal carpal joints. On the

radial side of the carpus, this is mostly produced by the trapezium and trapezoid sliding extensad on the scapholunar, though there is some movement of the trapezium flexing on the trapezoid. The surfaces between these two distal carpals and their corresponding metacarpals is too flat to allow much movement, but on the ulnar side of the carpus, about 50° of this flexion is produced by the metacarpals flexing on the carpals, and only 20° by the magnum and unciform sliding extensad on the scapholunar.

Deviation is also a complicated movement, involving all the joints. Although the joint between the radius and scapholunar resembles that in fissipedes, little deviation, only about 100, occurs here in pinnipedes. The majority of deviation (50° in Phoca, 30° in Pusa) is produced at the mid and distal carpal joints. As in flexion, on the radial side, it is the trapezium and trapezoid which slide radiad on the scapholunar to give ulnar deviation, while on the ulnar side the movement is produced by each metacarpal rocking onto its ulnar side. This curious movement makes the digits on the ulnar side seem longer in ulnar deviation; the claws are in a straight line in ulnar deviation, but subequal, with digit 1 appearing the longest, in the straight position (fig. 15, p. 62). These movements give a total deviation range of about 60° (in Phoca, less in Pusa) with the long axis of metacarpal 1 travelling from 150-750 ulnar deviation relative to the radius. This same movement of the ulnar metacarpals enables them to be abducted from the radial ones, so that, from a position parallel to metacarpal 1, the long axis of metacarpal 5/diverges 500.

Backhouse states that the manus acts as a hydroplane during swimming, and is carried in ulnar deviation, which is also made clear by the photographs

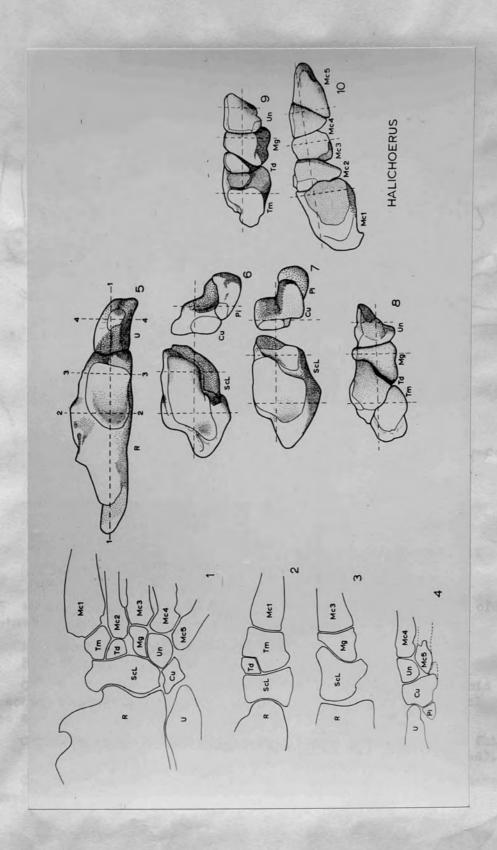


Fig. 14 Carpal diagram of Halichoerus.

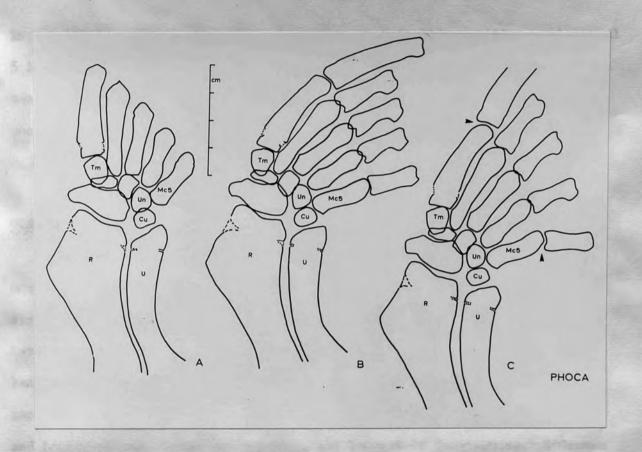


Fig. 15 Action in the carpus of a phocid. Drawn from radiographs of an immature Phoca.

- A Extensor view, radial deviation.
- B Extensor view, ulnar deviation, digits adducted.

Compared with A, the movement of the trapezium and trapezoid on the scapholunar can be seen, also the approximation of metacarpal 5 to the cuneiform.

C Extensor view, ulnar deviation, digits abducted (i.e. flipper spread).

so ments in tudentially of little use on land, being sta

Compared with B, most of this movement occurs at the metacarpophalangeal joints.

in Ray (1963). The account above indicates that in this position, metacarpal 5 is deeply slotted into the ulnar border of the carpus, between the cuneiform and unciform - (in the straight position it hardly touches the unciform). This is obviously a most stable position and provides a rigid hydroplane.

OMMATOPHOCA ROSSI

The Ross seal is particularly interesting because it represents the most extreme example of the specialisation of the forelimb along a line divergent from that of the more typical seals (Phocini). While most seals have a rather short flipper, of the type seen in Halichoerus, useful on land as well as in the water, the Antarctic seals (Lobodontini) show an increasing elongation of the flipper. The flipper is shortest in Lobodon and Leptonychotes, longer in Hydrurga, and longest in Ommatophoca. O'Gorman (1963) describes a sinuous type of locomotion occurring in Lobodon and Hydrurga on ice and shows that while Lobodon assists this locomotion with its fore-flippers those of Hydrurga are too long to help in this way. The hand of Ommatophoca is not only elongated, but the proportions of the digits have changed so that the first is much longer than the fifth (King 1965). In overall shape it thus tends to resemble that of a dolphin or an (Otarid) sea lion, and suggests a parallel locomotory function, the flipper being used more as a hydroplane or in a wing-like flapping action (see Ray's (1963) analysis of sea lions underwater,) than the paddle described by Backhouse (1961) for Halichoerus. The manus is undoubtedly of little use on land, being even longer than in Hydrurga.

The carpus of Ommatophoca is notable especially for the tightness with which the bones interlock, particularly those on the ulnar border. The forelimb thus forms the rigid hydroplane described by Backhouse (1961) for Halichoerus without being in ulnar deviation. This is especially evident in the shape of the cuneiform and the adjoining bones. As shown in both RUS and FES, the ulna ends in a rather flat surface, and the cuneiform is applied closely to this flat surface and one on the ulnar side of the radius (fig. 16, p. 66). Metacarpals 4 and 5 show similarly angular surfaces in RUS where they adjoin the cuneiform and unciform. The trapezoid and trapezium, which in Halichoerus articulate to a continuous concave surface on the scapholunar, have here separate articular facets. The proximal surface of the scapholunar presents a smooth convex condyloid surface on its ulnar side and a concave surface radially. This concavity represents, as in Halichoerus, the base of the tubercle, which is here almost directly radiad of the body of the scapholunar. The distal surface of the radius fits the scapholunar quite closely.

Movement at the carpus is thus necessarily limited. The main action is a combination of flexion with ulnar deviation, therefore equivalent to the propulsive flick which Backhouse describes in Halichoerus. The flexion is more extreme along the radial border of the hand than ulnad; measured between the long axes of the forearm and metacarpal 1, flexion is 55°, accompanied by 30° ulnar deviation. Metacarpal 5 is only flexed through 30°. The reverse movement can produce 20° of hyperextension, comparing metacarpal 1 and the forearm, and this also is less extreme on the ulnar side, metacarpal 5 attaining only 5° hyper-extension.

Flexion originates particularly at the joint of radius and scapholunar. The condyloid ulnar half of the scapholunar slides extensed and twists in the "cup" of the radius, and the radially placed "flat" slides flexad; this produces 20° of flexion, and the ylnar deviation. The trapezium slides flexad on the scapholunar (which is here slightly convex in FES) to give 25° flexion, and metacarpal 1 slides extensed to give a further 10° flexion. The trapezoid does not flex so far on the scapholunar (15°) as the trapezium, so there is some movement between them. The magnum does not flex on the scapholunar but is carried on it, moving past the unciform which slides extensed on a flat surface but flexes only 10°. The flexion at the ulnar side of the carpus is mostly due to the metacarpals flexing on the unciform. The metacarpals also converge when flexing, due to the distal facets of the distal carpal bones converging somewhat from extensed to flexad.

Hyperextension is the reverse movement, ending almost entirely on the scapholumar sliding, in the reverse direction, on the radius.

Some 40° of supination is possible, the radius moving on the ulna, and all the carpal bones with it.

The carpus of the sea leopard, Hydrurga, another of the Lobodontini, shows, particularly in the form of the scapholunar, a condition somewhat intermediate between Halichoerus and Ommatophoca. The concavity on the radial side of the proximal facet of the scapholunar and the corresponding facet of the radius are less completely on the radial side, and the distal facets for the trapezium and trapezoid are not so distinct as in Ommatophoca (fig. 16, p. 66).

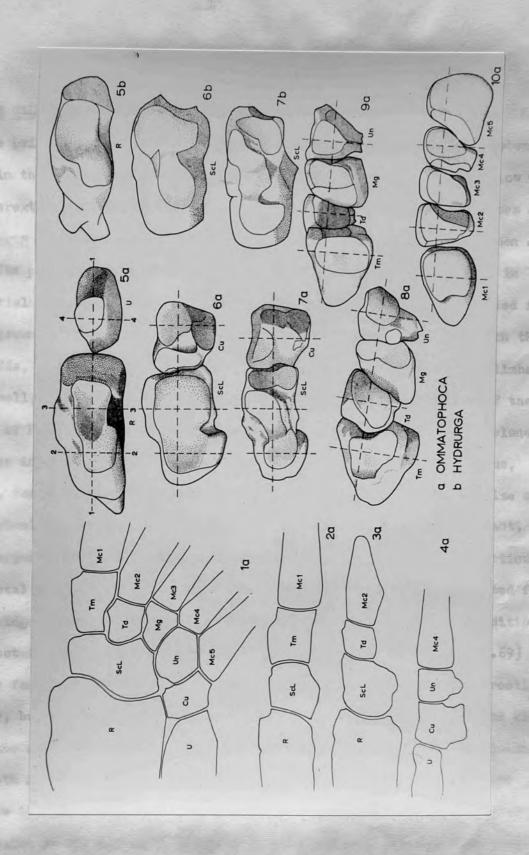


Fig. 16 Carpal diagram of Ommatophoca (a) and partial diagram for Hydrurga (b).

ZALOPHUS CALIFORNIANUS

The principal interest of the carpus of the Otariidae (and the Odobeni/dae, which in this respect are almost identical) lies in its ability to allow the 90° hyperextension used by these forms when on land. Backhouse describes how Halichoerus bears its weight upon the distal ends of the metacarpals when on land. The position of the hand is therefore essentially digitgrade as in terrestrial carnivores. In the Otariids, the palm of the hand is applied flat to the ground, from the carpo-metacarpal joint distally. They are, with the Odobeni/ds, perhaps the only carnivores to have truly plantigrade forelimbs.

Howell, (1928), briefly considered the carpus in his comparison of the anatomy of Phocid and Otariid pinnipedes, and indicates that the scapholunar is larger in the Otariidae. His subsequent reasoning is quite erroneous, however, for he ascribes this relative enlargement to an increase in size of the proximal facet to take the radius in terrestrial locomotion. In fact, the enlargement concerns mostly the radial side of the scapholunar, particularly the distal facet for the trapezium and trapezoid. This is a complicated facet, with a ridge running obliquely from extenso-ulnad to flexo-radiad. Additionally the facet is concave along the plane of this ridge (see RUS fig.17, p.69) so that the facet is saddle shaped. Finally, this facet does not face directly distally, but is turned extensad, more so on the radial side than on the ulnar side - the saddle is spirally twisted. The proximal facet of the scapholunar is a smooth convex shape, fitting the distal concavity of the radius; the curvature is much greater in the radio-ulnar than the flexor-extensor plane.

Flexion at the carpus in Zalophus is rather slight by comparison with the Phocids, attaining only 20°. Ray (1963) shows that the forelimbs of the

Otariids is used as a paddle or "wing" for swimming, the whole limb being flapped from the shoulder in a manner reminiscent of a bird flying. This would require a firm carpal joint.

The 90° hyperextension necessary for terrestrial locomotion is achieved in a unique fashion. On the radial side of the carpus, the main movement occurs between the scapholunar, proximally, and the trapezoid and trapezium. These two distal carpal bones slide radiad along the curved face of the scapholunar, thus causing 30° ulnar deviation, and also, because of the twist in this face, 80° hyperextension (fig. 18, p. 70). On the ulnar side of the carpus, the cuneiform slides proximally to lodge between the ulna and radius, and the unciform similarly moves proximally on the scapholunar. These movements give a firm ulnar border to the limb, and also correspond to the movement of the radial border into 300 ulnar deviation. The hyperextension at the ulnar border occurs between the unciform and metacarpals 4 and 5, the curved (in FES) proximal surfaces of the metacarpals allowing them to slide flexad on the unciform until their extensor surfaces are in contact with the unciform. The hinge for this hyperextension is thus somewhat oblique, running from the mid-carpal joint on the radial side to the carpo-metacarpal (distal carpal) joint on the ulnar side. The magnum lies across this hinge; 70° of hyperextension occur between the scapholunar and the magnum and a further 20° between the magnum and metacarpal 3. Additionally the magnum rocks on the scapholunar into radial deviation, and metacarpal 3 slides ulnad on it - these movements are part of the shortening of the ulnar side of the carpus necessary for ulnar deviation. There is 10° hyperextension of metacarpal 2 on the trapezoid.

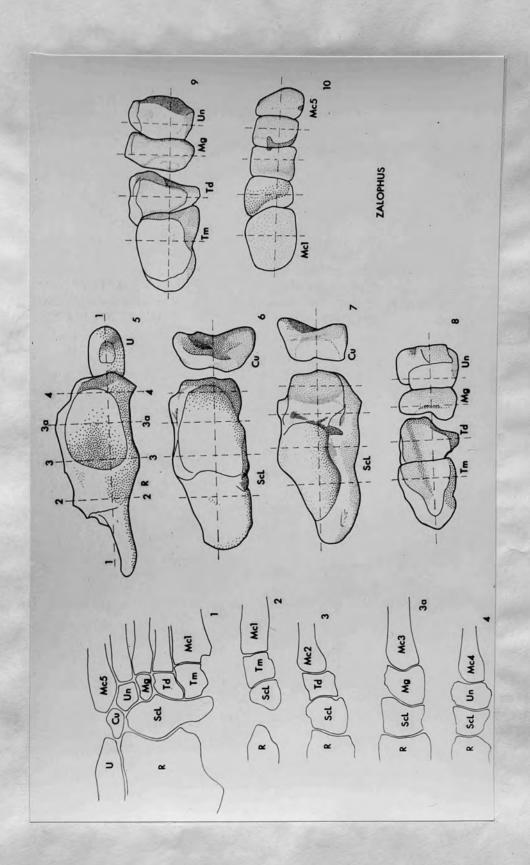


Fig. 17 Carpal diagram of Zalophus.

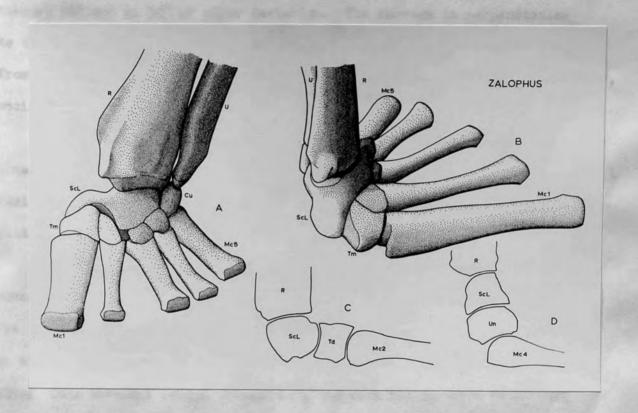


Fig. 18 Carpus of Zalophus in the terrestrial position.

- A In oblique extensor view.
- B In radial view.
- C RUS through radial side of carpus.
- D RUS through ulnar side of carpus.

There is little hyperextension of the scapholunar on the radius, or of the magnum and unciform on the scapholunar. Most of the movement is of the trapezium and trapezoid on the scapholunar, and of metacarpals 3 and 4 on the magnum and unciform.

The result of these movements is a manus hyperextended on the forearm through 90° and in 30° of ulnar deviation. The forearm is perpendicular to the ground when seen anteriorly, but inclined 30° posteriorly when seen from the side. The main weight is transmitted from the radius to scapholunar, unciform and the heads of metacarpals 4 and 5.

Deviation occurs mainly as a result of the scapholunar sliding radiad or ulnad on the radius, and attains 20° ulnar deviation (forearm v. metacarpal 1). Additionally, radial deviation may occur due to the trapezium and trapezoid sliding ulnad on the scapholunar.

Some axial rotation is also possible; as in most mammals, this is a movement of radius on ulna, and all the carpal bones move with the radius. The spinning movement required between the carpus and the ulna is provided at the proximal joint, the cuneiform sliding on the styloid process of the ulna. This movement ranges through 40°, and when the forelimb is serving as a hydroplane presumably alters the angle of attack to give a diving or surfacing movement. It is interesting to note that this rotation can still occur with the hand in the terristrial position, which could be of some importance in terrestrial locomotion.

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UNGULATE GROUPS

The ungulate groups have tended to concentrate on producing flexion movements at the carpus; this is at the expense of deviation, which in other animals is probably correlated with the use of the hand for holding food and climbing. This does not mean, however, that the flexion produced is a straight one; as already indicated, there is an important deviational component accompanying it, and the various groups of ungulates show interesting differences in the way this is produced.

PERISSODACTYLA

Material:-

Tapiridae;

Tapirus sp. - tapir - skeletal only

Rhinocerotidae;

Rhinoceros sumatrensis - Sumatran rhinoceros - skeletal BM(N.H.) 1949-1-11-1

Ceratotherium simum - White rhinoceros - fresh dead

Equidae;

Equus caballus - horse - skeletal and fresh dead.

Also incomplete remains of various fossil perissodactyls;

Hydrachyus BM(N.H.) M. 3809 and Aceratherium BM(N.H.) (Rhinocerotidae)

Hipparion BM(N.H.) M. 14732, Anchitherium BM(N.H.) M. 5752 (Equidae)

and various specimens of

<u>Palaeotherium</u> spp. BM(N.H.) M. 30028, 30089, 29744, 28243, 28234, 2484, 2485. (Palaeotheriidae).

RHINOCEROTIDAE

The distal surface of the radius in the rhinoceroses can be divided into two functional areas (fig.19, p.74). On the ulnar side there is a concave facet which receives the convex proximal surface of the lunar. The radial side is more complicated, a convex in FES, on the extensor side. The proximal surface of the scaphoid is complementary to this, and the joint surface is S-shaped in FES. The distal surface of the ulnar bears a small rather flat surface on its radial side which abuts the lunar and presumably acts as a mechanical stop. The rest of the surface, for the cuneiform, is saddle shaped, convex in FES, but concave in RUS as the ulnar margin of the bone is produced into something of a styloid process.

The mid-carpal joint provides five joint surfaces. The distal surface of the scaphoid bears two surfaces, a strongly convex (in FES) surface for the trapezoid and a rather flat facet on the ulnar side which in fact acts as a stop facet for the magnum. The lunar similarly bears two surfaces, one, strongly concave in FES and RUS, for the magnum, the other rather flatter, a stop facet for the unciform. Lastly, the cuneiform bears a concave (in FES) surface for the unciform.

Flexion reaches 140°, of which 90° occurs at the proximal joint. Here, the cuneiform slides flexad round the ulna, but because of the projection of the styloid process of the ulna at the ulnar-flexor angle, the cuneiform also slides somewhat radiad, inside this projection. This radiad movement pushes the whole of the carpus to the radiad side. The scaphoid slides flexad round the radius on the broad convex facet at the flexor side. The lunar is

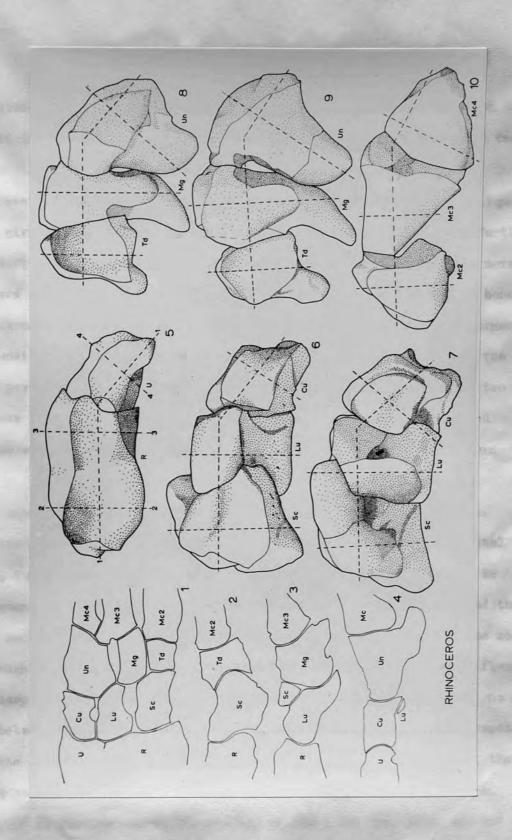


Fig. 19 Carpal diagram of Rhinoceros

caught between these movements, and has no equivalent facet around which to slide; it is instead lifted clear of the radius, moving with the other two bones.

The overall effect of this flexion at the proximal joint is an oblique hinging, giving ulnar deviation with flexion, for the scaphoid slides further, round a larger convexity, than the cuneiform. With such a complicated movement, there is a certain amount of readjustment of the proximal row of bones between themselves, and, in particular, small facets at the proximal corners of the cuneiform and scaphoid adjoining the lunar which are evident in the extended position are not apparent in flexion, due to abduction of the two outer bones from the lunar. This movement accounts for the wedge shaped appearance of the lunar in surface, extensor, view commented on by Osborn (1929).

The mid-carpal joint exhibits rather more straight-forward flexion.

Because the proximal row as a whole moves into oblique flexion, the distal surfaces, for the distal row of bones, remain level with each other. The main movements are the magnum flexing on the concavity of the lunar, and the unciform on the cuneiform; the stop facets for these bones, between the scaphoid and the magnum, and the lunar with the unciform, are out of contact in flexion. The metacarpals are gorried on the magnum and unciform, with virtually no flexion between them and the carpals, except for metacarpal 2 on the trapezoid. Because the distal surface of the scaphoid for the trapezoid is convex, the trapezoid cannot move the full 40° flexion with the other distal carpals, instead, 20° of flexion occurs between the scaphoid and trapezoid, and 20° between the trapezoid and metacarpal 2.

EQUIDAE

The carpus of Equus is considered next, as it provides the greatest contrast within the Perissodactyla to the rhinoceroses, yet obviously works on the same functional pattern.

The carpal bones are fully described by Sisson and Grossman (1953) but the salient features, from the point of view of this study, are repeated here (fig. 20, p. 77).

The distal surface of the radius can be divided into three facets, one for each of the proximal carpal bones. That for the scaphoid is the largest, rather flat in RUS, but S-shaped, that is concave extensed, convex flexed, in FES. The opposing surface of the scaphoid matches at least the more extensed part closely. The surface for the lunar resembles that for the scaphoid in FES but the concave, flexor, part is not so large, and there is consequently a large step on the radius between these two facets. The surface for the cuneiform, which represents the distal end of the ulna fused to the radius, is simply concave in FES, but almost flat in RUS.

The mid-carpal joint differs somewhat from that of the rhinoceros. The distal surface of the scaphoid is flat extensed, as a stop joint for the magnum, but concave flexad for the trapezoid. The lunar similarly has a flat surface extensed, divided between facets for the magnum and unciform, and a concavity flexad for the magnum. The distal surface of the cuneiform is strongly concave in FES for the unciform.

Flexion attains 140° - 150°, which is in fact enough to fold the limb completely at the carpus to achieve a lying position because the forearm skeleton is bowed throughout about 30°. 50° of carpal flexion occurs at

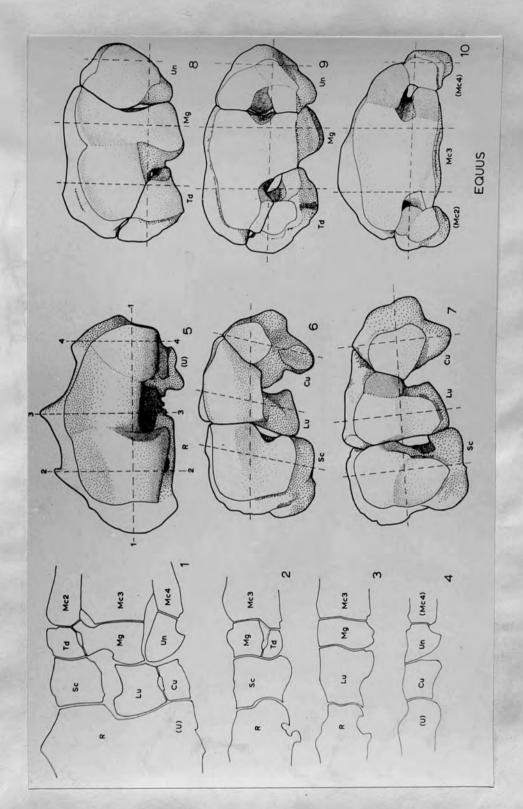


Fig. 20 Carpal diagram of $\underline{\text{Equus}}$

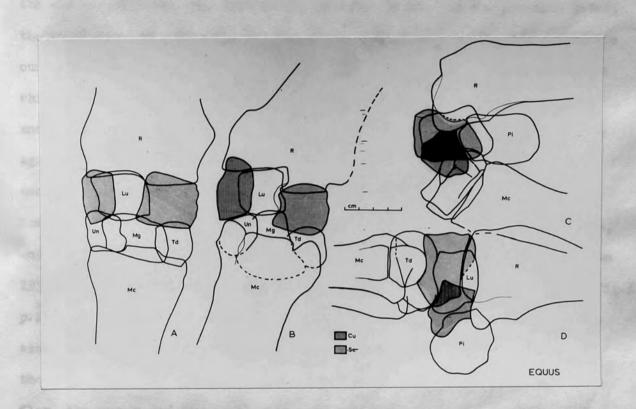


Fig. 21 Action of the carpus of Equus, drawn from radiographs.

- A Extensor view, carpus extended.
- B Extensor view, carpus flexed. The extent to which the scaphoid and lunar pass each other in flexion is noteworthy. The oblique surface which the proximal bones provide for the distal bones (un, mg, td.) to flex on is also evident.
- C Radial view, carpus flexed.
- D Radial view, carpus extended. The extent of flexion at proximal and mid-carpal joints can be seen, also the different surfaces of the radius for the three proximal carpal bones.

the mid-carpal joint, the rest at the proximal joint. At the proximal joint, the scaphoid slides flexad round the appropriate facet on the radius, and the cuneiform similarly slides round at the ulnar side of the radius. As in the rhinoceros, this means that the proximal row is flexing on two high sides, and the lunar is lifted virtually clear of the radius, being in contact only against the side of the step. This flexion is straight, that is, is not accompanied by deviation, due to the "flat" slope of the radius (in RUS). However, with the scaphoid travelling round the higher surface of the radius. and the lunar flexing with the cuneiform (as described by Sisson and Grossman 1953), the resultant surface on which the distal row must flex is stepped (fig. 6, p. 20). Thus the trapezoid flexes on the concavity of the distally projected scaphoid, while the magnum flexes on the lunar, and the unciform with it on the cuneiform; this does produce ulnar deviation with flexion. As they so flex, the magnum and trapezoid also rock more onto their ulnar sides. The distal row bones are closely bound to each other, however, and there is no movement between themselves, or between them and the metacarpal.

These two types, the horse and rhinoceros, show the main principles of carpal action in the perissodactyls, particularly in the action of the proximal row. The majority of perissodactyls agree essentially with the rhinoceros type; this includes the tapirs, the fossil rhinoceros Aceratherium, and the palaeotheres. The fossil Equidae, on the other hand, Hipparion and Anchitherium, agree in the form of their carpus with the modern horse.

A third type of perissodactyl carpus is seen in the fossil "running rhinoceros" Hyrachyus (fig. 22, p. 80) and also, to judge from the drawings

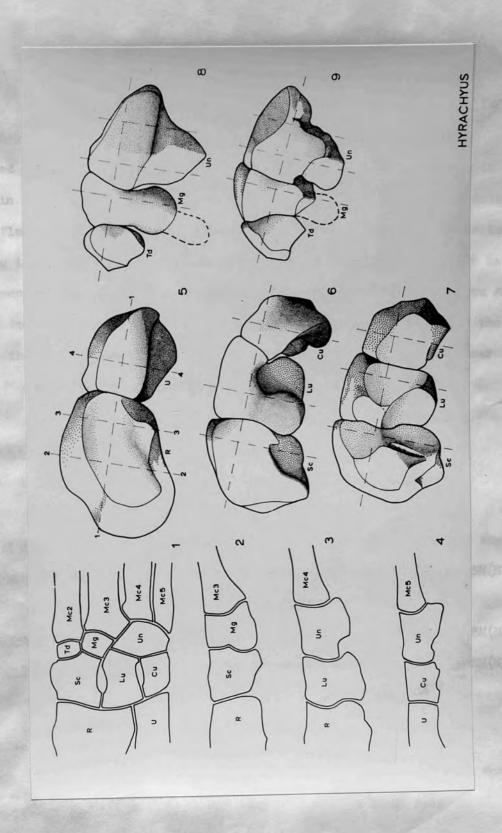


Fig. 22 Carpal diagram of Hyrachyus.

of the articular surfaces given by Osborn (1929), the titanotheres. In these forms, the articulation between the radius and lunar is better developed on the flexor side, so that the lunar remains in contact with the radius in flexion. As a correlative, the scaphoid is rather less developed on the flexor side, particularly along the ulnar margin adjoining the lunar, enabling it to rock into ulnar deviation during flexion. This change in the arrangement of the proximal row means that the lunar and scaphoid flex more or less together. This is reflected in the proximal articulation of the magnum, the more flexor facet of which, instead of flexing on the lunar alone, flexes on a bowl formed by both lunar and scaphoid.

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ARTIODACTYLA

Material:- tak surface of the fund radius and also is starply divided by

Suina; nto separate facets for each of the bonne of the proximal rew. As

Sus scrofa - pig - fresh dead and skeletal

Phacochoerus aethiopicus - warthog - skeletal only BM(N.H.)

1962-12-4-1 with

Hippopotamus amphibius - hippopotamus - skeletal only BM(N.H.) 726j

Choeropsis liberiensis - pigmy hippopotemus - skeletal only BM(N.H.)

distally past the ounsiform or its ulmer side (see RDS) 1952-4-1-4 the surface

Ruminatia;

Ovis aries - sheep - fresh dead and skeletal

Capreolus capreolus - roe deer - fresh dead

end, and haring a contextly extensed functioning as a stop against the

Dama dama - fallow deer - fresh dead

Tylopoda;

Also the fossils

Samotherium BM(N.H.) M4265 (Giraffidae)

Oreodon culbertsoni BM(N.H.) M573 (Oreodontidae)

RUMINANTIA

The carpus in the different ruminants appears to be very uniform in struuture and mode of action. The sheep (fig. 23, p. 84) may be taken as a typical example.

The distal surface of the fused radius and ulna is sharply divided by ridges into separate facets for each of the bones of the proximal row. As seen in FES, each of these facets is S-shaped, concave at the extensor margin and convex flexad. The facets run obliquely across the distal surface of the radio-ulna, and the ridges between them project at the flexor margin separating strong indentations which accomodate the scaphoid, lunar and cuneiform in their flexed positions. The styloid process of the ulna projects distally past the cuneiform on its ulnar side (see RUS). As both the surface view and RUS show, the facet for the scaphoid is higher, that is, more distally and flexad produced than that for the lunar, and the lunar facet similarly projects more than that for the cuneiform. The proximal facets of the scaphoid, lunar and cuneiform match the distal surface of the radio-ulnar closely in FES, each having a convexity extensad functioning as a stop against the

appropriate concavity of the radio-ulnar, and a concave face extensad functional in flexion. In surface view, the appearance, particularly of the lunar and cuneiform, is rather more complex. The lunar has effectively three facets, the concavity extensad and two convex facets flexad, one for the side of the ridge on the radius between the scaphoid and lunar facets, the other for the ridge between the lunar and cuneiform facets. The cuneiform has the convexity of the extensor margin extended as a ridge along the radial border of the bone's proximal surface, while the ulnar side slopes steeply away down the ulnar side of the bone as a surface abutting the projecting styloid process of the ulna.

The mid-carpal joint is somewhat less complex, essentially, mimicking the proximal joint with an S-shaped form in FES. The trapezoid and magnum are fused, giving a bone with two proximal facets, one for the scaphoid, one for the lunar. Both are concave extensed, curving into convex surfaces flexad (FES fig. 23,2, p. 84) but that for the lunar projects further proximally, and the scaphoid is appropriately "countersunk" where it adjoins the lunar to allow this projection to slide into flexion. The proximal surface of the unciform similarly bears two facets, one for the lunar and one for the cuneiform. The flexor half of the facet for the cuneiform slopes away on its ulnar side, allowing the bone, in flexion, to slide inside the projecting heel of the cuneiform.

Flexion in the ruminants reaches 165°, of which about 90° occurs at the proximal joint and 75° at the mid-carpal joint. Flexion at the proximal joint is rather complicated, as each of the proximal bones flexes on its own "track". The cuneiform slides radiad and flexes "inside" the styloid process of the ulnar (fig. 24, p.85). As the more extensor part moves furthest radiad, this

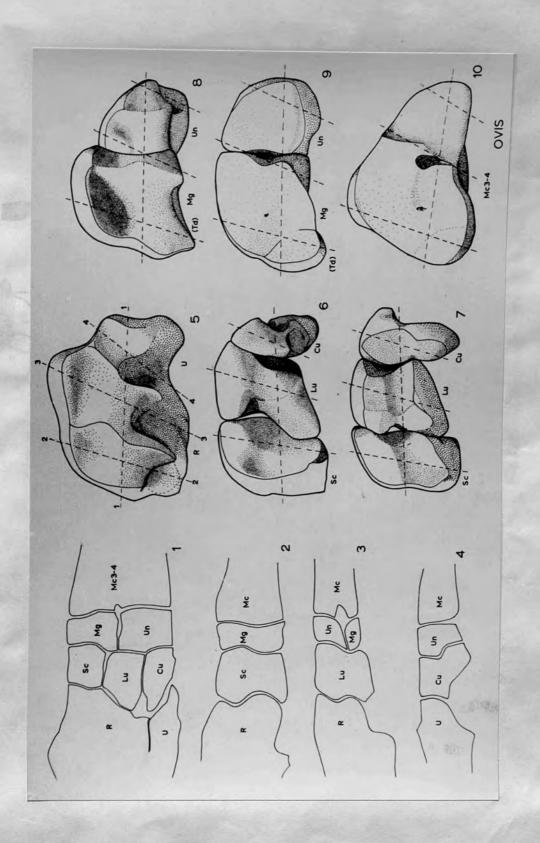


Fig. 23 Carpal diagram of Ovis.

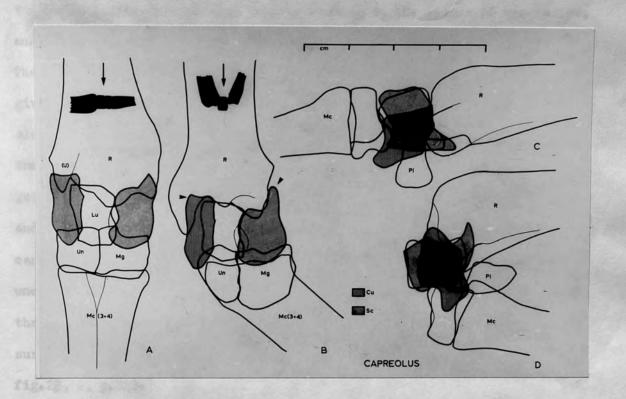


Fig. 24 Action of the carpus of an artiodactyl. Drawn from radiographs of Capreolus.

- A Flexor view, carpus extended.
- B Flexor view, carpus flexed. The extent to which the three proximal bones move radially can be seen, and also the extent to which they move relative to one another. The apparent radial deviation of the metacarpal is an illusion due to the angle of photography.
- C Radial view, carpus extended.
- D Radial view, carpus flexed. The extent of flexion at the proximal and mid-carpal joints can be seen.

is a spiral movement, and gives ulnar deviation with flexion. Similarly, the lunar slides into flexion largely resting on the ridges of the radius, and since that on the radial side is higher, also gives ulnar deviation. The scaphoid also follows this spiral movement, and the net effect is to give about 30° ulnar deviation with the 90° flexion. With each bone moving along its own course, there is considerable readjustment between them, and the need for three separate bones is evident. Flexion at the mid-carpal joint is more straightforward, the magnum-trapezoid flexing on the scaphoid and the unciform on the lunar. Because of a projecting heel, the unciform can only flex through 55°, and 20° of flexion therefore occurs between the unciform and the metacarpal, since the metacarpal is carried on the magnum through 75° flexion. The flexor border of the metacarpal and the opposing surface of the unciform are appropriately curved to facilitate this (FES fig. 25, 4, p. 84).

SUINA

The carpus of, for example, <u>Sus</u> (fig.25, p.87) resembles very closely that of a ruminant. The distal surface of the radius and ulna presents the same three oblique facets for the scaphoid, lunar and cuneiform. The most conspicuous difference lies in the lesser development in <u>Sus</u> of the indentations along the flexor margin of the distal surface of radius and ulna. This necessarily limits the amount of flexion possible at the proximal joint to about 60°. Flexion at the mid-carpal joint is also much restricted, partly by a similar lack of undercutting at the flexor margin of the magnum and unciform, partly because the facets active in flexion are less highly curved. The magnum flexes through 40°, carrying the metacarpals with it.

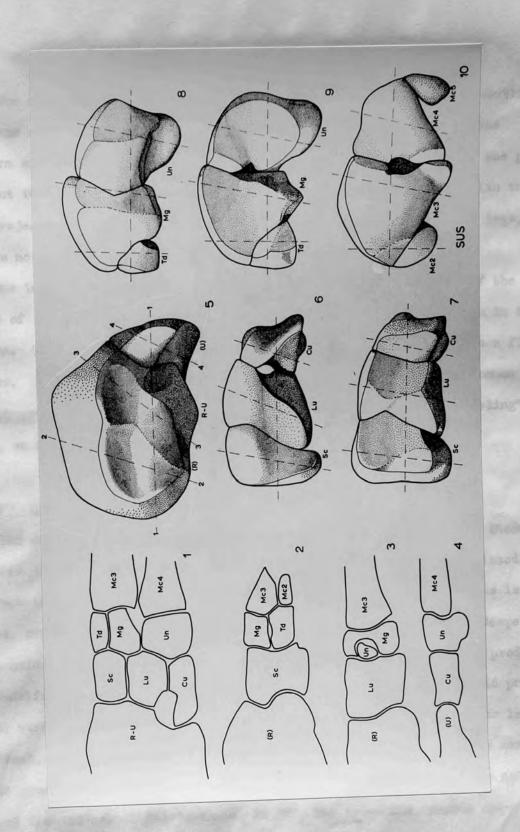


Fig. 25 Carpal diagram of Sus.

As in the ruminants, the unciform cannot flex so far as the magnum, abutting the lunar after only 30° flexion, and 10° of flexion occurs between the unciform and metacarpal 4. Flexion at the carpus is thus limited in the pig to about 100°, which explains why sleeping pigs lie on their sides with their legs projecting sideways along the ground; equally, with such short legs, they do not need to fold them up after the fashion of a ruminant.

One interesting feature is the presence on the flexor surface of the radius of a small stop-facet which receives the heel of the cuneiform in full flexion. This facet is better developed in <u>Phacochoerus</u>, where it is a flat surface. It is presumably correlated with the habit, particularly common in <u>Phacochoerus</u>, of walking around or digging with the tusks, in a "kneeling" (i.e., on flexed carpus) position.

HIPPOPOTAMUS

The carpus of <u>Hippopotamus</u> (fig. 25, p.89) appears to exaggerate those features of the artiodactyl carpus which contrast with that of a perissodactyl. By comparison with <u>Sus</u> the spiralling of the lunar facet of the radius is more marked, and the apex, the extensor and ulnar end of the groove much deeper. The proximal surface of the lunar is correspondingly more proximally produced. The cuneiform is relatively rather larger than in <u>Sus</u>, and the styloid process of the ulna less prominent. The scaphoid on the other hand, is rather less important, and in particular does not have a convex (in FES) extensor margin on the proximal surface as a stop-facet. This lack of stop-facets is notable also at the mid-carpal joint, where, in FES, the trapezoid, magnum and unciform all have convex proximal surfaces which fit concave surfaces on the scaphoid,

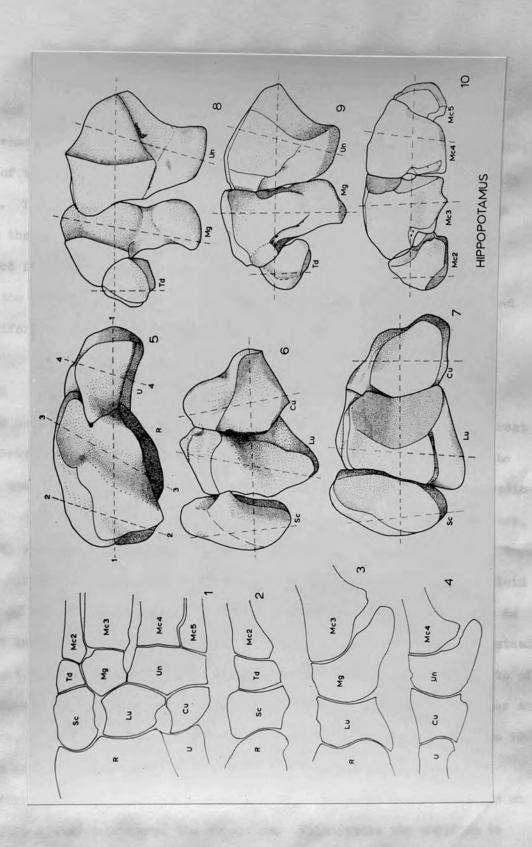


Fig. 26 Carpal diagram of Hippopotamus.

magnum and unciform.

Flexion at the proximal joint reaches only 60° (as in <u>Sus</u>). The spiral action of the flexing lunar and cuneiform adds 30° ulnar deviation to this flexion. The scaphoid slides on a separate course from the lunar, though flexing the same amount, and its distal surface for the magnum becomes separated from that of the lunar. 40° flexion occurs at the mid-carpal joint, the trapezoid sliding on the scaphoid, the magnum on the lunar, and the unciform on both lunar and cuneiform.

TYLOPODA

The carpus of the Camelidae (Llama, fig. 27, p. 94) differs from the rest of the Artiodactyla in a manner which parallels the difference between the Equidae and the rest of the Perissodactyla. The distal surface of the radioulnar presents the same three facets, for the scaphoid, lunar and cuneiform, each well demarcated by ridges. However, the oblique, spiralled form of these facets characteristic of other artiodactyls is not apparent, and the styloid process of the ulna does not project ulnad and flexad of the cuneiform. As evident in the surface views (fig. 27, 5, p. 94) the proximal joint is instead a straight flexion hinge. Greater development of the convex flexor facets of the radio-ulnar, and lesser projection of the heels of the scaphoid, lunar and cuneiform, allows more flexion to occur at the proximal joint, in fact to 120° (instead of 90° in a ruminant). At the mid-carpal joint, the trapezoid articulates to the scaphoid as a ball in a cup, while the unciform flexes on the sloping distal surface of the cuneiform. This causes the unciform to slide radiad and somewhat proximally in flexion, while the trapezoid stays at

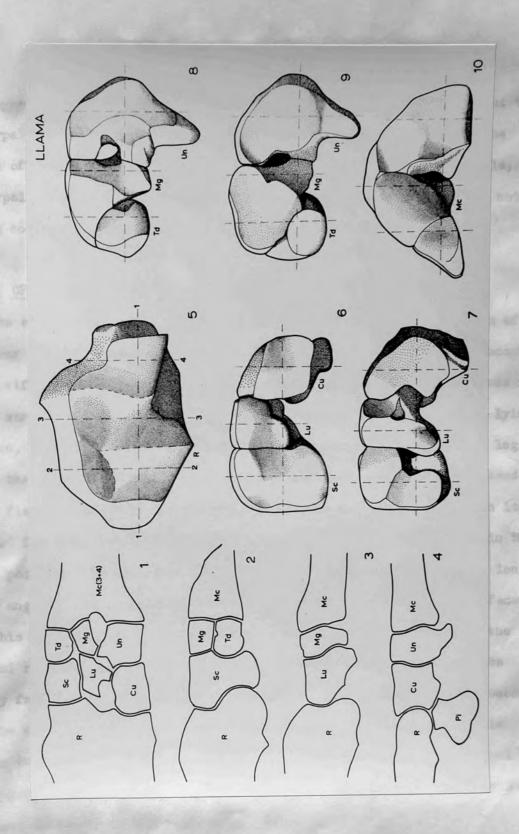


Fig. 27 Carpal diagram of Llama.

its "higher" level, and provides 20° ulnar deviation with 50° flexion at the mid-carpal joint. The magnum is lifted almost clear of the lunar by the flexion of the bones on either side of it. As in the other articlactyls, the metacarpal 4 flexes 10° on the unciform to compensate for the unciform not flexing so far on the cuneiform as the trapezoid does on the scaphoid.

SUMMARY OF THE ARTIODACTYL CARPUS

The artiodactyl carpus is essentially based on the spiral rotation of the lunar and cuneiform, in contrast to the perissodactyls, where the scaphoid and cuneiform provide the main hinge. It seems probable that differences in carpal structure explain the old question of horses getting up, from a lying position, front legs first but cattle hind legs first. In rising hind legs first, the weight of the animal rests, once the hind legs have been extended, on the flexed carpus - to use the popular expression, the animal is "on its knees". The artiodactyl carpus seems to provide a much firmer carpus in the flexed position than does that of the horse (it is of course, only the longer legged ungulates which fold up their fore-legs completely, and so are faced with this problem). This is partly due to the interlocking ridges of the proximal row, but the instability of the equid carpus in flexion results largely from the form of mid-carpal hinge. In view of this, it might seem that the carpus would be unstable in the Camelidae (which get up and lie down in the same way as the rest of the Artiodactyla), but the mid-carpal hinge, particularly between the cuneiform and unciform, seems a tighter joint with less curvature in the radio-ulnar plane.

(fig. 28, p. 94) though the radi SUBUNGULATA from extended to flexad. Both are

This is a somewhat heterogenous superorder including the Proboscidea, Hyracoidea, Sirenia and the extinct Embrithopoda. Though the Sirenia might more usefully be compared to the Pinnepedia, the others make a comparison with the other ungulates, and so the group is included here.

conver in FEG, the ulna being much sore sharply curved along its flaxor edge.

Material:-

Proboscidea;

Loxodonta africana - African elephant - skeletal only BM(N.H.)

1961-8-9-82

Hyracoidea;

Dendrohyrax validus - Tree hyrax - skeletal only BM(N.H.)
97-3-14-7 and 10-6-11-2

Sirenia; to in the from of a desper our flexad on the proximal bases with

Dugong sp. - Dugong - skeletal only BM(N.H.) 1534c

Trichechus sp. - Manatee - skeletal only BM(N.H.) 1338c

Embrithopoda;

Arsinoitherium zitteli - - skeletal only, several specimens in BM(N.H.) (listed in Andrews, 1906) including M.8836, M.9433, M.9095, M.9096

Proboscidea

The distal surfaces of the radius and ulna are of almost equal size

(fig. 28, p. 94) though the radius is larger from extensad to flexad. Both are convex in FES, the ulna being much more sharply curved along its flexor edge. The ulna has a small flat locking facet for the lunar at its radio-extensor corner. The distal surface of the radius is scarcely differentiated into separate facets for the scaphoid and lunar, and is gently convex in RUS; the ulna is gently concave. The proximal surface of the scaphoid is rather small, relative to the other two bones of the proximal row. The lunar has a flat proximal surface in RUS, but is gently concave in FES, and has a small flat surface at the ulnar-extensor corner to oppose the complementary facet on the ulna. The cuneiform is convex in RUS, rather more curved than the ulna, so parted from it ulnad.

The distal surface of the proximal row provides a smooth concave surface in RUS which is matched by a convex proximal surface on the bones of the distal row. As shown in FES, but more clearly in the surface views (figs. 28; 7,8,p. 95) this joint is in the form of a deeper cup flexad on the proximal bones with a shelf around the extensor margin.

Flexion at the carpus in the elephant is limited to 90°, all of which occurs at the proximal joint. The lumar has to slide further than the cuneiform, and as well as flexing, the bones spin somewhat in axial rotation. The scaphoid is on the outside of this rotation and is almost lost from the radial border of the carpus - indeed the lunar, in rotating, sweeps over nearly all of that facet of the radius on which the scaphoid sits in extension. The net result of this movement is to give some 10° ulnar deviation in addition to the flexion. That the fore-foot is turned outwards is confirmed by the photographs in Muybridge (1957 pl.112) where the palmar surface is clearly visible, pointed obliquely

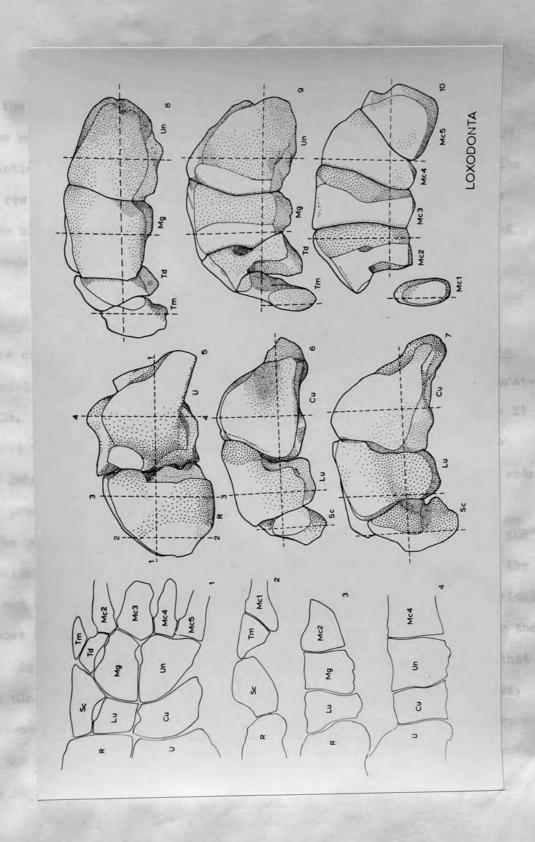


Fig. 28 Carpal diagram of Loxodonta.

toward the camera, in direct side views.

The mid-carpal joint seems incapable of flexion, but can produce 20° of deviation, from 10° radial deviation, to 10° ulnar deviation, with the distal row sliding ulnad and radiad on the proximal row. It is possible that the ulnar deviation accompanies flexion, but this requires verifying from fresh material.

HYRACOIDEA

The carpus of <u>Dendrohyrax</u> (fig. 29, p. 97) resembles that of <u>Loxodonta</u> in general form, the one obvious difference being the presence of a separate centrale. Eales (1929) found the centrale in an embryo <u>Loxodonta</u>, where it was fused to the scaphoid and therefore on the proximal side of the mid-carpal joint. By contrast the centrale of <u>Dendrohyrax</u> is on the distal side of the proximal joint.

The proximal joint of <u>Dendrohyrax</u> is rather more irregular than in the Proboscidea, with an oblique ridge running across the distal surface of the ulna, and the radius protruding further distally than the ulna. In particular, the facet of the radius for the scaphoid protrudes further than that for the lunar. In FES the distal surface of the radius is gently concave, and that of the ulna similarly curved but with the oblique ridge already mentioned. The mid-carpal joint presents a very smooth curve in RUS, but not a steep one, with the proximal bones presenting a concavity and the distal bones convex. In FES as well, the proximal bones present a gently concave distal surface.

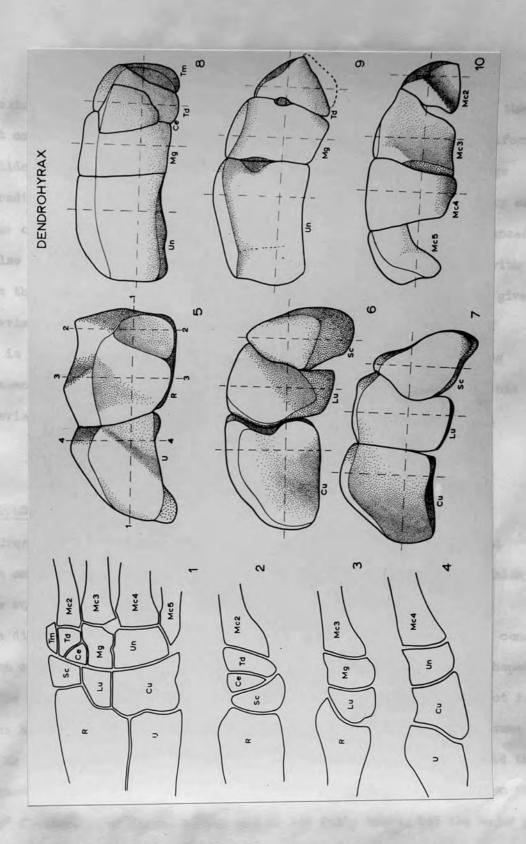


Fig. 29 Carpal diagram of Dendrohyrax.

Flexion reaches 90°, from 20° hyperextension, with the majority of the movement occurring at the proximal joint. The scaphoid, lunar and cuneiform first slide extensad, for 50° flexion, then rock gently on the flexor edge of the radius and ulna to give a further 40° flexion. With the obliquity of the ridge on the ulna and the matching groove on the cuneiform, the extensad slide also involves a radiad movement of the cuneiform, which, coupled with the fact that the lunar and cuneiform are flexing on the "high" radius, gives ulnar deviation with flexion. At the mid-carpal joint, a further 20° of flexion is possible, and the joint is also a deviational hinge, providing 30° movement from 10° radial to 20° ulnar deviation. Some at least of this ulnar deviation occurs in conjunction with the flexion of the mid-carpal joint.

EMBRITHOPODA - ARSINOTHERIUM

Andrews (1906) describes the known carpal bones of Arsinotherium and comments on their general similarity to those of proboscideans, a conclusion which is endorsed by the present study.

The distal surface of the radius (fig. 30, p.99) changes from deeply concave near the extensor edge to convex towards the flexor side, therefore S-shaped in FES. The distal surface of the ulna resembles this shape in section, but is much less strongly curved. Flexion at this joint obviously follows the same pattern as in Loxodonta, with the scaphoid and lunar sliding further round the radius than the cuneiform slides round the ulna, so giving ulnar deviation with about 80° flexion. The distal carpal row is not fully known, but the major part, that is, the magnum and unciform, presents a smooth convex surface in RUS, to the

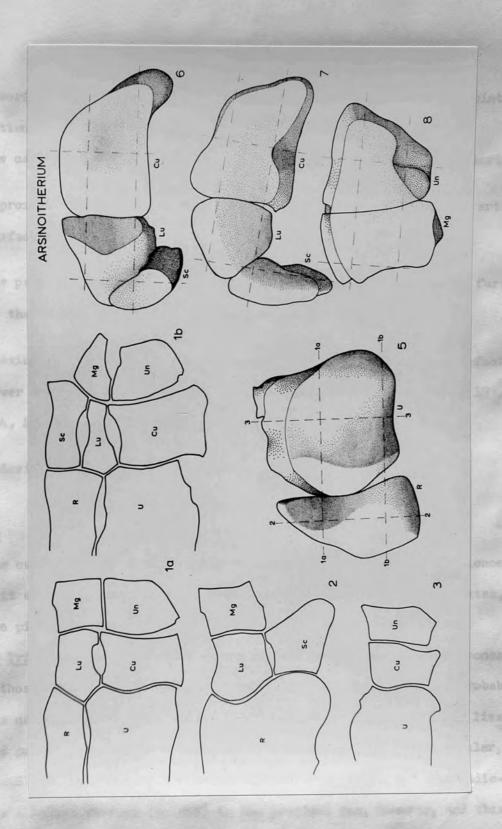


Fig. 30 Carpal diagram of Arsinoitherium.

distal surface of the proximal row, suggesting that the mid-carpal joint is a deviational hinge as in proboscideans.

The carpus in these subungulates may be summed up therefore as having:-

- 1) A proximal joint in which the ulna forms as large a part of the articular surface as the radius.
- 2) The proximal joint as a flexion hinge in which the lunar slides further, on the radius, than the cumeiform does on the ulna.
- Flexion limited to 90°, and the lineage presumably always short-footed, never having required to fold the carpus completely (see Grassé 195, (fig. 484, 486) comparing the lying positions of elephant and camel)
- 4) A deviational hinge at the mid-carpal joint.

SIRENIA

The carpus of the sirenians might be considered here for convenience, though it obviously compares in function not with the other subungulates, but with the pinnipede carnivores.

In <u>Trichechus</u> (fig. 31, p.101) the carpus is composed of seven bones, though those of the distal row are tightly bound by ligaments, and probably there is no movement between them. The trapezoid is very small, and lies extensed on the trapezium. In general form the bones are rather angular, both in RUS and FES, recalling somewhat the carpus of Ommatophoca. The radio-ulnar presents a convex surface (in FES) to the proximal row, however, and this obviously provides a flexion hinge. Flexion is in fact limited to 40°, and

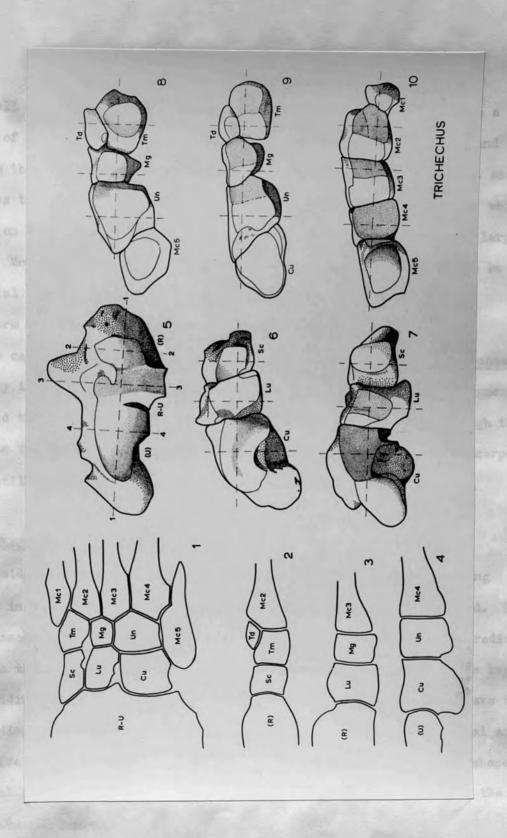


Fig. 31 Carpal diagr am of Trichechus.

nearly all this occurs at the proximal joint. The cuneiform flexes on a surface of tighter curvature than the lunar, causing ulnar deviation and increasing the angle of attack of the flipper. (The similar movement in seals decreases the angle of attack of the flipper, because the scapho-lunar while flexing on a "higher" surface as in <u>Trichechus</u>, also flexes through a larger angle). Movement at the mid-carpal joint is very slight, and seems to be only axial rotation, the unciform sliding extensad and rotating on the cuneiform while the trapezium slides flexad on the scaphoid.

The carpus of <u>Dugong</u> (fig. 32, p. 103) differs from that of <u>Trichechus</u> primarily in the fusion of the elements. The scaphoid and lunar are generally fused and the distal row of carpal bones are also fused into one, though the facets on the distal surface, even that between the trapezoid and metacarpal 2, are still distinguishable.

THE UNGULATE CARPUS IN SUMMARY

Considerable emphasis has been placed in this review on the varying methods in which ulnar deviation, to accompanying flexion, is produced. In the perissodactyls, the scaphoid slides round a larger surface on the radius than does the cuneiform on the ulna; in artiodactyls, the lunar is the key bone, sliding round a spiral groove in the radius; the subungulates have the lunar riding over a higher surface on the radius, but there is no spiral action. These differences are summarised by fig. 33, (p. 105) which compares the shape of the distal surface of the radius and ulna and the movements thereon of the proximal carpal bones.

The main rôle, never-the-less, is to provide a flexion hinge which folds

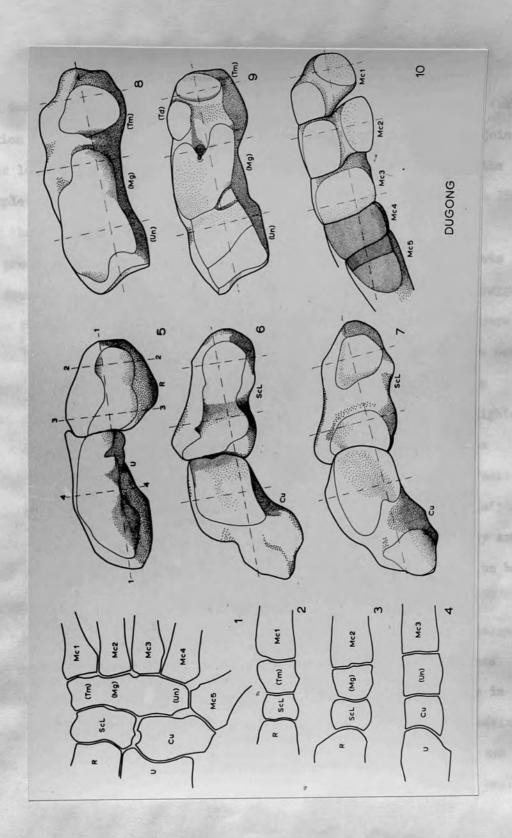


Fig. 32 Carpal diagram of Dugong.

the wrist during the recovery phase of limb use. In the shorter footed forms, this flexion is around 100°, and is produced primarily at the proximal joint. The longer legged forms, Equidae, Camelidae and Ruminatia have to fold the wrist completely, through the functional equivalent of 180°, in order to lie down, and the mid-carpal joint is increasingly important.

The presence of stop facets at the extensor edge of the carpal joints has been frequently mentioned. The use of the term 'stop-facet' might suggest that these facets are subject to repeated concussion, and Dr. K.M.Backhouse (pers. comm) has pointed out that bone could not withstand this. As the carpal bones close to the extended position, with these stop facets coming into operation, so the ligaments on the flexor side of the carpus would be tightening, and would be just as important in stopping the movement, as well as responsible for slowing it. In a mechanical sense, however, the stop facets do prevent hyperextension at the carpus, and lock it in the extended position, so that the term "stop-facet" is convenient in this sense. Because they are in contact when the wrist is extended, the stop facets are also liable to be the main weight transference areas.

One further point which requires some comment is the presence of large hook-like processes on the flexor side of the magnum and unciform in some forms. Osborn (1929) drew attention to the presence of these processes in the carpus of titanotheres, and suggested (p.775) that they were a cursorial adaptation acting as levers pulled by the flexor muscles of the wrist, and his fig. 704 suggests that the <u>flexor carpi radialis</u> inserted onto the hook

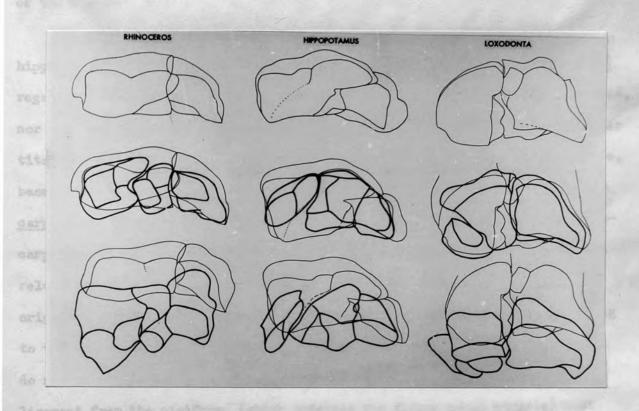


Fig. 33 Comparison of the proximal joint of the carpus in Perissodactyla (Rhinocerus), Artiodactyla (Hippopotamus), and Proboscidea (Loxodonta). The upper row shows the appearance of the distal surface of the radius and ulna. In the middle row, the outlines of the bones of the proximal row have been added, positioned as in extension. In the lower row, the proximal bones are shown positioned as in flexion.

This shows the differences in importance of the part of the radius on which the scaphoid articulates, and the extent to which the three proximal carpal bones move independently of each other.

1942) provides some programmer. Though such hyperextension was not.

apparent during exactnation of the from Seal shincoares lieb, it was not

possible to subject this to the same force that would be operative buring

of the magnum.

In fact, these hooks are well developed in tapirs, rhinoceroses, hippopotamus, Oreodon, and similar forms, but in the animals most usually regarded as cursorial, horses and ruminants, these processes are not developed, nor are they apparent in the gravigrade forms (as Osborn noted for the heavier titanotheres). Osborn's reconstruction of the musculature of the titanothere, based presumably on the knowledge of tapirs and rhinoceros, shows the flexor carpi radialis inserting at the usual position in mammals, the bases of metacarpals 2 and 3. Further, Osborn himself cites (op. cit. p. 716) the correct relationships of these tuberosities to surrounding structures, as points of origin for some of the flexor ligaments and some of the short muscles running to the toes. Certainly the muscles usually regarded as flexors of the wrist do not attach to the magnum at all, and the unciform only receives a small ligament from the pisiform, (which receives the flexor carpi ulnaris) most of the ligaments from this last running to metacarpal 4. It seems that these hooks are found in those forms where stop facets are not so well developed, and particularly where the distal carpal joint is still curved (in FES), not flattened. In these circumstances there is some possibility of hyperextension, and the flexor ligaments may be of increased importance in preventing it; or possibly, instead, the hyperextension is encouraged, and elastic contraction of the ligaments (as described by Camp and Smith, 1942) provides some propulsion. Though such hyperextension was not apparent during examination of the fresh dead rhinoceros limb, it was not possible to subject this to the same force that would be operative during galloping. Analysis of cine film of a galloping rhinoceros suggests that

such hyperextension may occur; and the flexor hooks certainly receive much of the flexor sheet of ligaments.

The primates may be examined next as an example of a group which has specialized at the carpus in the opposite direction to the ingulates, that is, for producing deviational movements rather than flexion.

illustrated by considering the grang on a borniator rail of a can running upstairs. The hard is placed on the rail about of the body in sharp ulner deviation, and as the body as a whole moves past the hand, the wrist awings into radial deviation; during the whole of this time the wrist is also hyperextended. This type of novement must occur in all forms which grasp a branch as they walk along it, including the majority of prinates and the sloths, but not the tree-runners ("marcheurs" of anthony, 1912) such as squirrels, marmonets and variety carnivores. It is, of course, a novement of the body over a fixed part of the limb, and comparable with the hyperextension which occurs in terrestrial forms at the metacarpe-phalangeal joint.

Material:

iomo magismu

Pongo pysassus - orang-otan - skeletal only, BM(N.H.)

1948-10-25-1

Gorilla gerilla - gorilla - skeletal culy, hkild.

195,940,43-6

Hylobates sp. - gibbon - abeletel only, inc. BK(Walls)

1890-11-22-56

PRIMATES

The primates may be examined next as an example of a group which has specialised at the carpus in the opposite direction to the ungulates, that is, for producing deviational movements rather than flexion.

The importance of deviation for arboreal forms can be most readily illustrated by considering the grasp on a bannister rail of a man running upstairs. The hand is placed on the rail ahead of the body in sharp ulnar deviation, and as the body as a whole moves past the hand, the wrist swings into radial deviation; during the whole of this time the wrist is also hyperextended. This type of movement must occur in all forms which grasp a branch as they walk along it, including the majority of primates and the sloths, but not the tree-runners ("marcheurs" of Anthony, 1912) such as squirrels, marmosets and various carnivores. It is, of course, a movement of the body over a fixed part of the limb, and comparable with the hyperextension which occurs in terrestrial forms at the metacarpo-phalangeal joint.

Material:

Homo sapiens	- man	- skeletal only
Pongo pygmaeus	- orang-utan	- skeletal only, BM(N.H.)
		1948-10-25-1
Gorilla gorilla	- gorilla-	- skeletal only, BM(N.H.)
		1948-4-3-6
Hylobates sp.	- gibbon	- skeletal only, inc. BM(N.H.)
		1850-11-22-56

Mandrillus leucophaeus - drill - fresh dead and skeletal BM(N.H.)

1948-5-21-2

Papio sp. - baboon - fresh dead and skeletal BM(N.H.)

de no character and a later an

Ateles sp. - spider monkey - ligamentary skeleton

Lemur catta - ring tailed

lemur - skeletal only BM(N.H.)

The vertical part | 1948-10-18-1

Propithecus sp. - sifaka - skeletal only BM(N.H.)

HOMO SAPIENS

The carpus of man is naturally the best known of the primates. Apart from the very full descriptions of the bones and ligaments in the standard anatomy text books, (e.g. Johnston, T.B., et.al. 1958), Wright (1935), Johnston (1907) and Virchow (1899) have considered the functional movements of the bones, and Gilford et.al. (1941) have added a mechanical interpretation.

From the point of view of this study, the essential feature of the human carpus is the curved surface provided at both proximal and mid-carpal joints in both flexion and deviational planes (fig. 34, p. 111). The distal surface of the radius is a smooth concave curve in FES, and is matched by the convexity of the lunar and scaphoid. A similar concavity in RUS is interrupted by a shallow ridge running from flexad to extensad. At the midcarpal joint, a similar concavity is provided by the distal surface of the proximal row for the magnum and unciform. The trapezoid and trapezium are excluded from this joint in RUS, articulating to the distal surface of the scaphoid on a separate

facet from that for the magnum. Leboucq (1884) showed by sectioning embryonic material that the human scaphoid was actually a compound bone formed by the fusion of a scaphoid and centrale (though I regard most of the bentralia" he described from adult skeletons as neoplastic nodules), and cites Henke and Reyer (1874) as finding the same thing. The distal surface of the scaphoid to which the trapezium and trapezoid articulate is evidently the radio-distal facet of a triangular centrale, and the magnum abuts the ulnar-distal surface.

The various published accounts of the movements of the carpal bones disagree somewhat amongst themselves, Wright's (1935) account in particular suggesting rather more hyperextension, and rather more movement between the scaphoid and lunar, than the others. However, a general account may be given, based on these various papers and especially the radiographs in Gray's Anatomy (Johnston T.B., et.al. 1958).

Flexion reaches about 70°, and involves both mid-carpal and proximal joints. The lunate and cuneiform slide extensed on the radius (and on the cartilage between the radius and ulna), thus flexing about 15° (Wright says 30°, but this is not confirmed by his own radiographs). Rather more flexion occurs at the mid-carpal joint, with the magnum and unciform sliding extensed on, mostly, the lunar to give 60° flexion. The proximal-distal length of the scaphoid is such that the trapezium and trapezoid are distal to the "axis of rotation" of the magnum (the "axis of rotation" being simply the geometrical centre of the curvature of the distal surface on the lunar) and slide flexad into flexion on the convex surface of the scaphoid. As this surface is less sharply curved than the distal surface of the lunar, and the distal bones are therefore able to flex less far on the scaphoid (45°) than does the magnum on the lunar (60°), the

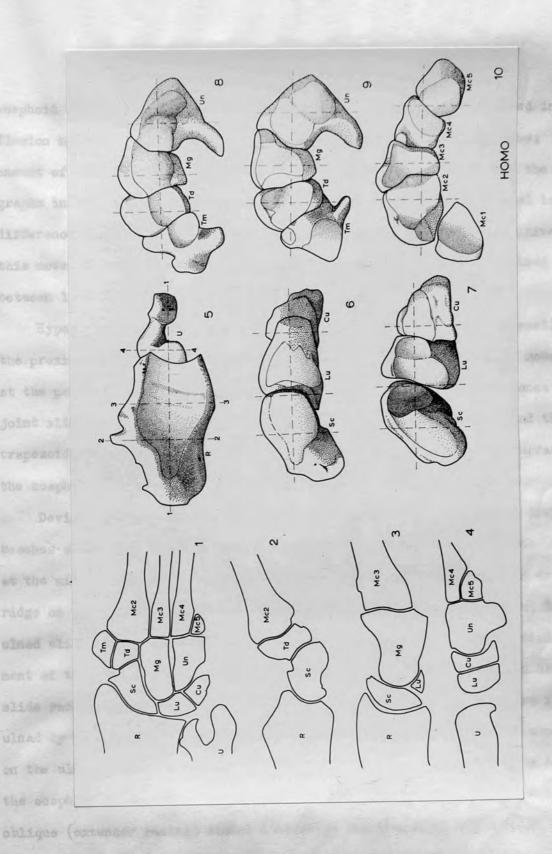


Fig. 34 Carpal diagram of Homo.

scaphoid flexes further than does the lunar. Presumably it is pushed into flexion by the trapezium and trapezoid pressing on the distal surface; the amount of movement between the scaphoid and lunar, about 15°, (from the radiographs in Gray's Anatomy - Wright's radiographs suggest 40°) is equal to the difference in movement between the magnum and trapezoid. In a primitive carpus this movement would have been between the scaphoid and centrale instead of between lunar and scaphoid.

Hyperextension is the converse of flexion, and takes place primarily at the proximal joint. Total hyperextension is about 50°, with 30° of movement at the proximal joint and 20° at the mid-carpal joint, the distal bones at each joint sliding flexad on the proximal bones. Again, the trapezium and the trapezoid are an exception, sliding extensad on the convex distal surface of the scaphoid.

Deviational movements also involve both carpal joints. Radial deviation reaches about 200, ulnar deviation to about 300. Radial deviation is produced at the mid-carpal joint, since the scaphoid rests against the flexor extensor ridge on the radius even in the straight position. The main movement is the ulnad slide of the proximal end of the magnum, and the resultant radiad movement of the distal end, which abuts the scaphoid. The trapezium and trapezoid slide radiad across the distal surface of the scaphoid. The unciform is pushed ulnad by the head of the magnum, and becomes widely parted from the cuneiform on the ulnar side. As noted by Johnston, H.M. (1907), and in Gray's Anatomy, the scaphoid is somewhat flexed in radial deviation, due to the pressure on its oblique (extensor facing) distal surface by the trapezium and trapezoid.

In ulnar deviation, most of the movement occurs at the proximal joint,

as the scaphoid and lunar slide radiad on the radius (the lunar crosses the flexor-extensor ridge). This movement provides about 25° of the ulnar deviation, and the rest is produced at the mid-carpal joint. The head of the magnum slides radiad to abut the ulnar side of the radius, and the trapezium and trapezoid slide ulnad across the distal surface of the scaphoid. The unciform slides radiad with the magnum until it meets the lunar, and closes up to the cumeiform on the ulnar side.

Though these movements of the human carpal bones are well known, they seem not to have been related previously to the shapes of the articular facets in this way. Johnston's account comes nearest to doing so. The axes of rotation given by Wright are evidently the geometrical centres of curvature of these facets, though they were not so regarded by him. Perhaps the most striking case where this coint has been overlooked is Jones' statement (1942 p.71) that the large size of the magnum reflects the need to provide a firm base for metacarpal 3. In fact, the large size of the magnum provides an adequately large curved proximal surface, to give a flexion and deviation hinge at the mid-carpal joint. By restricting this joint in the deviation plane to the magnum and unciform, and effectively excluding the centrale, trapezium and trapezoid, the chord of the deviational hinge is shortened, and its curvature increased.

Although axial rotation, that is pronatory or supinatory movement, is primarily a movement of the radius around the ulna, it must affect the ulnar side of the wrist. All carpal bones move with the radius in rotation, so that the tissues connecting the ulna and cuneiform must get spirally twisted. The usual explanation (Hughes, 1944) given for the loss of the articulation between

the ulna and cuneiform, in man, is that it permits freer ulnar deviation. This may be a factor, but it is quite feasible to have the joint surface between the ulna and cuneiform on the same plane of curvature as the rest of the proximal joint - the giant anteater, for instance, (see later, p.126) has a very good articulation here and can produce as much ulnar deviation as man. One important factor is that the forelimb is no longer weight bearing (though the anthropoid apes show similar reduction of the ulna, and can walk on all fours). It seems to me very probable that the principal factor involved in man and the anthropoids is the extreme amount, 180°, of axial rotation which can be produced. A conventional joint between the ulna and cuneiform would be bound by joint capsule and this would necessarily be stretched by the twisting movement. Reduction of the joint between the bones, to a ligament which will readily twist and untwist, would simplify this.

PONGIDAE

The carpus in <u>Pongo</u> (fig. 35, p. 115), <u>Gorilla</u> and <u>Pan</u> resembles that of <u>Homo</u> very closely in both morphology and function. The major functional difference is the restricted amount of hyperextension possible, only 15°-20°. Straus (1940) has stated that this is due to the shortness of the long flexor tendons, but it is certainly reflected also in the restricted articular facets on the extensor side of the proximal row of bones. The main morphological distinction is provided by the presence, in <u>Pongo</u> only, of a separate centrale. This results in the scaphoid moving in flexion with the lunar, with the centrale flexing further on the scaphoid, instead of the scaphoid having to flex more than the lunar. In radial deviation, also, the centrale moves on the scaphoid, sliding

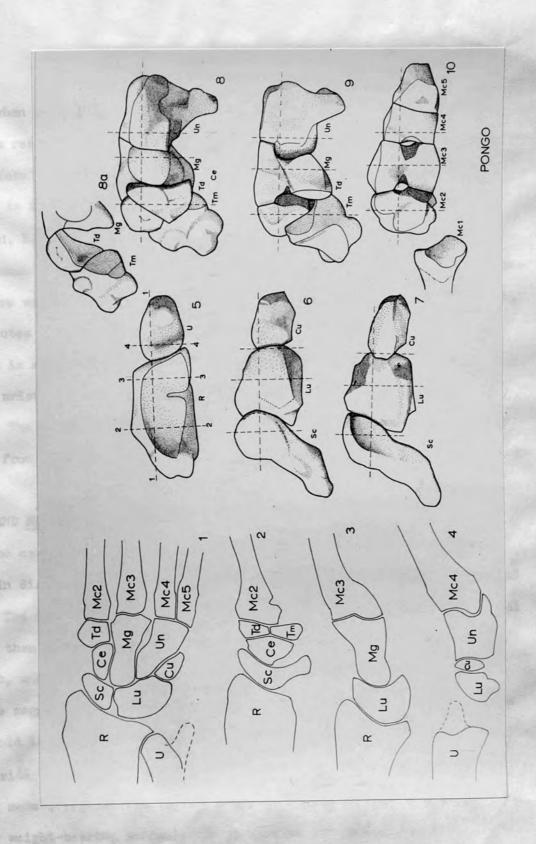


Fig. 35 Carpal diagram of Pongo.

radiad when pushed by the distal end of the magnum with the trapezium.

The restricted hyperextension in these forms is related to the use of the forelimbs for support when on the ground, as described by Straus. Flexion is freer than in man, 120° from the skeletal material of Pongo examined, but the total range of movement in the flexion-extension plane is not much greater. The movements are produced just as in man. The some-what more enlarged proximal end of the magnum in Pongo, compared with man, contributes what greater freedom of movement exists.

It is surprising that larger deviational movements are not possible at the wrist of these animals, as this might be expected in brachiating forms. The range is, however, the same as in man, a point made by Napier (1960) from observations of live animals, as well as from the present study.

PAPIO AND MANDRILLUS

The carpus of the baboons is essentially similar to that of Pongo, the main distinction being the good articulation between the cuneiform and ulna. The cuneiform itself is a larger bone, relative to the other carpal bones, than in the anthropoid apes (fig. 36, page 117). The centrale is present, and has a more acute angle between the two "distal" surfaces, those for the magnum and trapezoid. To match this, the proximal surface of the trapezoid is oblique - as seen in RUS, it runs from more distally on the ulnar side to more proximally on the radial side. The proximal joint is rather more irregular than in the other primates, perhaps to produce a firmer weight-bearing surface. In particular the radial margin of the radius projects distally into a depression on the scaphoid.

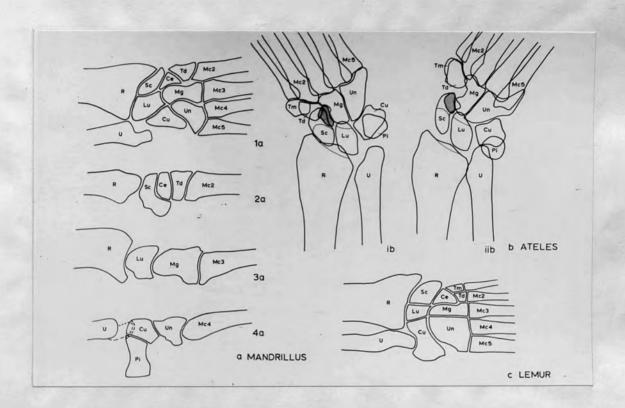


Fig. 36 Various primate carpi.

- a. Mandrillus, RUS and FES diagrams.
- b. Ateles, drawn from radiographs.
 - ib in radial deviation.
 - iib in ulnar deviation. There is considerable movement at the proximal joint (compare the position of the cuneiform relative to the ulna) and at the mid-carpal joint (note the approximation of the trapezoid to the scaphoid in ib, and of the unciform and lunar in iib). The position of the centrale (shaded) in radial deviation, projecting into the 'notch' in the magnum, and its radial movement in ulnar deviation, pressed by the 'head' (proximal end) of the magnum can be seen.
- c. Lemur, RUS of carpus, showing the large unciform, relative to the small magnum, together forming the convex mid-carpal joint surface.

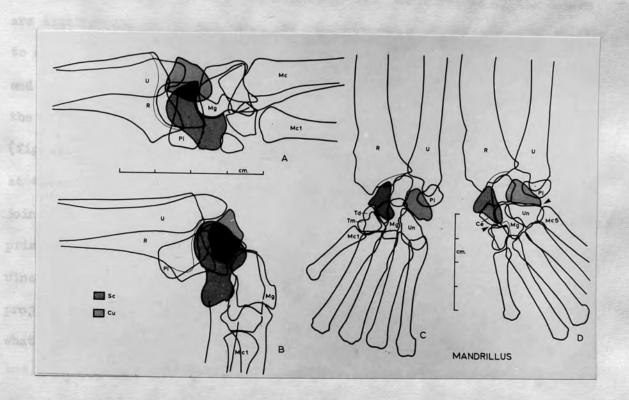


Fig. 37 Action of the carpus of Mandrillus. Drawn from radiographs.

- A Radial view, carpus extended.
- B Radial view, carpus flexed. Both proximal and mid-carpal joints contribute to the flexion, and the scaphoid is not parted from the radius in flexion, as is the scapholunar in a carnivore.
- C Extensor view, radial deviation.

a slightly radial shift of the centrals sorms I this scophold in Figure .

mutrels. It would suggether a from controls in the princips in correlated with

D Extensor view, ulnar deviation. The movement of the trapezium and trapezoid relative to the centrale, and of the unciform to the cuneiform can be clearly seen. There is also considerable movement of the scaphoid and cuneiform past the radius and ulna. As mentioned in the introduction (page 22), the forefeet of the baboon are digitigrade, not plantigrade, and hyperextension at the carpus is limited to about 20°. The metacarpus is thus held roughly in line with the forearm, and the hyperextension necessary between the vertical part of the limb and the part flat on the ground is produced at the metacarpo-phalangeal joint (fig. 37, page 118);120° of hyperextension can be produced here. Flexion at the carpus may reach 120°, of which 70° is produced at the mid-carpal joint, the rest proximally. The movements are produced just as in the primates already discussed. Full flexion is accompanied by about 20° of ulnar deviation, caused by the fact that the scaphoid flexes on the distally projecting radial margin of the radius, and by the cuneiform sliding somewhat proximally and "inside" (radially of) the styloid process of the ulna.

Compared with man, the total range of deviation, 50°, is about the same, but radial deviation being rather freer than in man. Movement at the proximal joint, due to the irregularity seen in RUS, is more restricted than in man, only about 15° of (ulnar) deviation being produced here. The range of movement at the mid-carpal joint is thus greater than in man, due particularly to the shape of the centrale and the bones articulating to it.

The presence of a free centrale in the baboons perhaps deserves some comment, No movement of this bone on the scaphoid could be discerned during deviation, either from the radiographs or from manipulating the fresh dead material, neither does it seem to flex on the scaphoid during carpal flexion. However, there is a slightly radial shift of the centrale across this scaphoid in flexion, apparently due to the bulbous head of the magnum pushing against the overlapping centrale. It would seem that a free centrale in the primates is correlated with

the greater freedom of movement at the mid-carpal joint consequent upon the proximal end of the magnum being more swollen.

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OTHER SIMIANS

In structure and function of the carpal, Ateles and Hylobates resemble each other closely, which is to be expected, as Erikson (1963) and others have emphasised their similarity on other features.

The main feature is an emphasis on deviation, which in these forms ranges through 65° - 70°. In this pliability, associated with their brachiating locomotion, they match the sloths (q.v. page 136). Structurally, their combines a hominal type proximal point with a mid-tarpel carpus, joint resembling that in the baboons. An acute-angled centrale, which fits tightly between the trapezoid and magnum in radial deviation, is present, and this is combined with a smooth (in RUS) proximal joint, comparable to that of man (fig. 36, page 117); the movement can be from 40° radial to 30° ulnar deviation. The form of the carpals in FES, and the range of flexion and hyperextension, are much as in man.

LEMURS

The carpus in the lemurs closely resembles that of other primates. The centrale is distinct in Lemur but fused to the scaphoid in Propithecus; the distal surface of the bone is rather less acute than in the monkeys, and resembles more the anthopoid apes in shape. The most distinctive feature of the lemuroid carpus seems to be the precise form of the mid-carpal joint. In the primates previously discussed, the proximal end of the magnum has provided the main deviational joint surface, and the unciform has adjoined this as a

widge on the ulnar side which is parted from the cuneiform in radial deviation, and closed to it in ulnar deviation. In the lemurs, the magnum and unciform together form a round proximal surface (in RUS), the major portion of which is provided by the unciform. Equally, the cuneiform shares in producing the cup, with the lunar and centrale, in which this convex surface slides (fig. 36, page 117).

Deviation is produced mainly at this mid-carpal hinge, as Hughes (1944) also noted. The full range is from 20° radial to 30° ulnar deviation (as in man) and all but 10° radial deviation is produced by the magnum and unciform sliding on the cuneiform, lunar and centrale. The other 10° radial deviation is produced at the proximal joint. Flexion and hyperextension each reach about 60°.

PRIMATE CARPUS IN SUMMARY

Essentially, the carpus of primates has four features:-

- 1) A moderate flexion-extension hinge at the proximal joint, where the bones of the proximal row slide extensad on the radius but do not part from it in extreme flexion on the extensor side;
- 2) A moderate flexion hinge also at the mid-carpal joint;
- 3) A deviational hinge at the proximal joint;
 - 4) And a deviational hinge at the mid-carpal joint in which the magnum and unciform slide on the proximal row of bones, but from which the trapezium and trapezoid are effectively excluded.

EDENTATA (XENARTHRA)

Material; war, and are not obliged to walk on its extensor surface.

Priodontes gigantea - giant armadillo - skeletal only BM(N.H.)

46-4-21-6 and 1963-2-5-1

(the last a "ligamentary skeleton" see p. 36)

Myrmecophaga tridactyla - giant anteater - fresh dead and skeletal material. BM(N.H.)

3-7-7-176

Tamandua tetradactyla - anteater - fresh dead and skeletal specimen BM(N.H.) 11-11-4-2

Scelidotherium leptocephala - ground sloth - (fossil) BM(N.H.) 37430

Megatherium sp. - ground sloth - (cast of fossil) BM(N.H.)

Choloepus sp. - two toed sloth - skeletal only BM(N.H.)

Bradypus tridactylus - three toed sloth - skeletal only BM(N.H.)

PRIODONTES AND A LINE OF THE PRIOR OF THE PR

To judge from the diagrams in Grassé (1955), the giant armadillo has in a number of ways the most extreme modification of the fore-limb among the armadillos. The middle finger is far larger than the other fingers, and includes an enormous ungual phalanx. This ungual phalanx is carried in a flexed position, and the animal walks on the extensor surface of the claw.

The ungual phalanges are enlarged on other armadilloes, and this is an obvious

fossorial adaptation. Except for <u>Tolypeutes</u>, which resembles <u>Priodontes</u> in this respect, (Grasse 1955), they do not have an excessively large middle finger, however, and are not obliged to walk on its extensor surface.

The ulna is a large bone, and ends distally in a condyloid, convex, surface which is somewhat elongate from the flexor to the extensor side. The proximal surface of the cuneiform is a similarly elongate concavity. By contrast with the ulna, the radius has a smooth concave distal surface with which the lunar articulates, but the flexor margin projects on the radial side as a ledge over which the scaphoid fits (FES fig. 38, p. 124). At the mid-carpal joint, the surfaces of the lunar and cuneiform are generally concave in FES, those of the magnum and unciform convex. The lunar has a flat extensor margin to its distal surface, which provides a stop facet for the magnum.

hyperextension to 60° flexion, shared equally between the proximal and mid-carpal joints. At the proximal joint, the cuneiform slides flexad down the ulna in flexion, and the direction of elongation of their articulation specifies the direction of the flexion plane. The lunar slides extensad in the cup of the radius, and remains in contact with the radius only on the ulnar side. The scaphoid slides flexad round the projecting lip of the radius. Flexion by the proximal row is limited to 10° by contact of the well developed flexor surfaces of the lunar and pisiform with the flexor surface of the radius. Flexion at the mid-carpal hinge is, like that at the proximal joint, oblique to the extensor margin of the bones; in fact, the flexion here is on the same plane as at the proximal joint. Both magnum and unciform slide extensad on the appropriate articular surfaces of the lunar and cuneiform, but the articulation

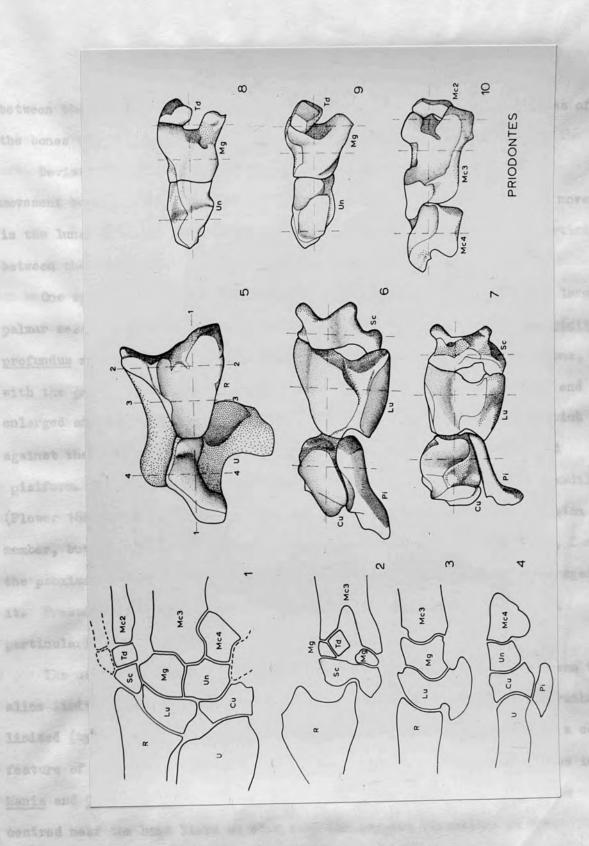


Fig. 38 Carpal diagram of Priodontes.

between the magnum and lunar is centred further from the extensor margins of the bones than that between the unciform and cuneiform.

Deviation at the carpus of <u>Priodontes</u> seems rather limited, to 15° movement between 15° and 30° ulnar deviation. The main feature of this movement is the lunar sliding ulnad or radiad on the radius. The shape of the articulation between the ulna and cuneiform limits the freedom of deviation.

One special feature of the skeleton of the hand in <u>Priodontes</u> is a large palmar sesamoid bone, apparently developed in the tendon of the <u>flexor digitorum profundus</u> muscle (Grassé 1955). This is an elongated, rather conical bone, with the pointed end at the distal interphalangeal joint. The proximal end is enlarged and tuberculated, with two flat surfaces on the extensor side which slide against the flat surfaces on the enlarged, flexor, side of the lunar and pisiform. The function of this sesamoid, which is found in all the armadilloes, (Flower 1885) is difficult to determine. Bone usually forms a compression member, but this sesamoid is hardly a prop between the finger and wrist, for the proximal end is shaped to slide past the wrist rather than to lodge against it. Presumably it acts as a lever system, during flexion of the finger, particularly perhaps from a hyperextended wrist position.

The carpus of <u>Priodontes</u> is morphologically rather complex, but seems to allow limited flexion and hyperextension, and a little deviation. The rather limited (by comparison with more normal tetrapods) amount of flexion is a common feature of rather specialised fossorial anteating forms, and is seen also in <u>Manis</u> and <u>Orycteropus</u>. The weight of the body in these forms tends to be centred near the hind limbs so that they can support themselves on their hind forelimbs for digging. During normal walking, the forelimbs are scarcely

needed for support, because of this posterior shift of the centre of gravity. Probably, they have a very small stride and the forelimb scarcely passes the vertical position during retraction, so that the wrist does not need to be folded to enable the foot to clear the ground during protraction.

This is undoubtedly a form where examination of fresh dead material would assist the interpretation. It is probable that considerable rotation movements can be produced, at least in the forearm, but this cannot be adequately evaluated from skeletal material.

MYRMECOPHAGA

The carpus in this animal resembles that of <u>Priodontes</u> in general form, but the mid-carpal joint is rather more complicated in shape and action.

The distal surface of the radius is gently concave in RUS, rather more acutely curved in FES (fig. 39 p.128). In addition, the extensor margin of the radius projects distally as a ledge overlapping the scaphoid extensad and radially so far that it reaches a ledge on the trapezoid. The scaphoid and lunar are similarly gently convex in RUS, more sharply convex in FES. The distal end of the ulna is a condyloid styloid process, and the cuneiform has a gently concave proximal surface which fits rather loosely to the ulna. At the mid-carpal joint, a somewhat spiralled surface is provided, resembling the proximal joint of the articulactyls. The scaphoid bears a ridge which articulates between the trapezium and the magnum, while the lunar similarly articulates between the magnum and unciform. Complementary to this, the magnum has a convex surface which articulates with the ulnar side of the scaphoid, and the unciform articulates to the lunar and cuneiform by a similar convexity. The unciform

has a flat surface on the ulnar side toward the extensor side which acts as a stop facet against a complementary flat on the cuneiform. The magnum and lunar have a similar stop facet extensad.

Myrmecophaga is another "anteating" form with enlarged claws on the forefeet, but does not have the heavy hind quarters, particularly not the heavy tail of Priodontes. It is more quadrupedal than the armadilloes or the pangolins, though it is capable of rearing onto its hind limbs as a defensive posture. The animal normally walks with the fore limb somewhat supinated, and the radial margin facing anteriorly. The enlarged claw of the third finger points 200 posteriorly of directly mediad, and the fingers are flexed so that the wight is taken on the extensor surface of the metacarpophalangeal joint. The claws of digits 1 and 2 are also enlarged (though not so large as that of digit 3) and in-turned, but digits 4 and 5 have reduced phalanges and the skeleton of the digits is directed distally to end inside two fibrous pads. There is no need for hyperextension between the fixed part of the foot on the ground and the limb moving over it as in (most) mammals with forward pointing claws, instead the foot rolls on the ground. As most mammals have the carpus slightly hyperextended when the limb is grounded, this being more stable for weight bearing, so in Myrmecophaga the carpus is normally 200 radially deviated during retraction, and 100 hyperextended.

The total flexion range of the carpus is 110° of which all but 10° is produced at the proximal joint. The movement at the proximal joint occurs in two stages. The first stage is a movement from the 20° radially deviated walking position of the hand to 30° ulnar deviation. This movement is produced by the scaphoid and lunar sliding to the radial side on the radius, and the

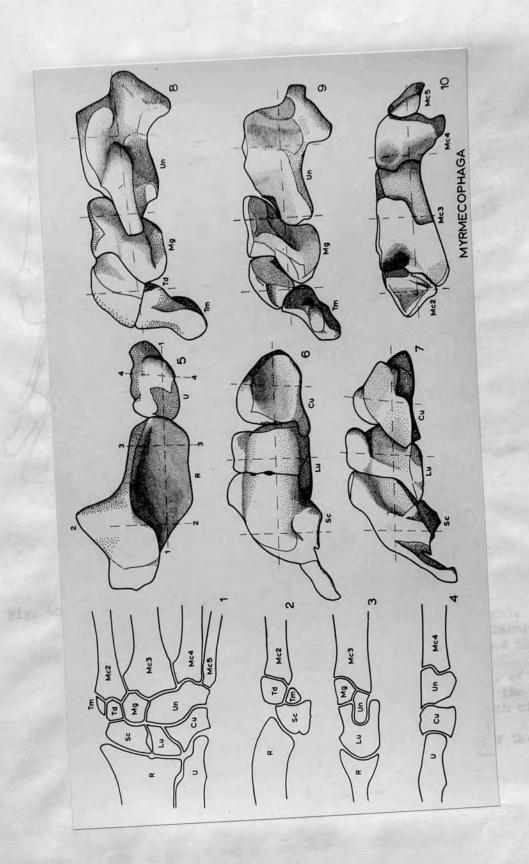


Fig. 39 Carpal diagram of Myrmecophaga.

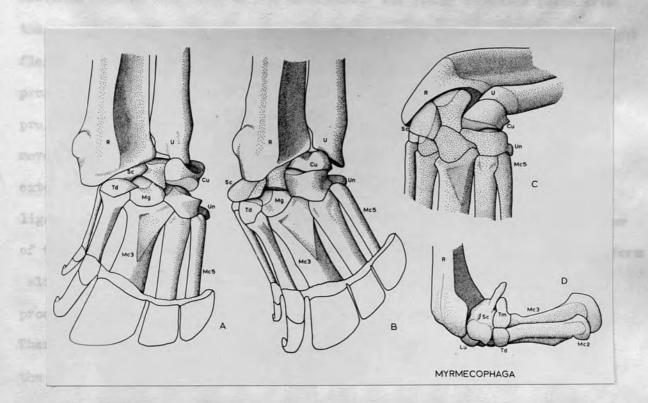


Fig. 40 Action of the carpus of Myrmecophaga.

A Extensor view, in radial deviation (walking position).

B Extensor view, in ulnar deviation. The scaphoid, lunar, and cuneiform have moved across the radius and ulna, and the unciform has closed up to the cuneiform.

C Oblique view, from distally of the radius and ulna, of the carpus in flexion. Most of the movement is due to the scaphoid and lunar flexing on the radius, exposing much of their proximal surfaces extensad.

D Radial view, carpus flexed, showing the position of the scaphoid on the projecting lip of the radius.

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unciform sliding with them on the cuneiform; the lunar therefore parts from the cuneiform. This movement is followed by a second stage, an almost straight flexion of the ulnar deviated carpus. This is also mainly produced at the proximal joint, by the scaphoid and lunar sliding extensad onto the distally projecting lip of the radius, (fig.40, p.129). The scaphoid particularly moves so far that large areas of its proximal surface are exposed radiad and extensad of the radius; further movement is limited by the radio-scaphoid ligament which runs obliquely from the radial border of the radius to the base of the tubercle of the scaphoid. On the ulnar side of the carpus, the cuneiform slides flexad on the ulna, and also slides somewhat radiad, as the styloid process of the ulna projects somewhat more on the ulnar side than radially. There is a small amount of flexion (10°) at the distal carpal joint between the carpal bones and the metacarpals.

The ability to apply the large claws to the ground in various directions is an important requirement of the hand in anteating forms. This depends on the rotational abilities of the forearm. In Myrmecophaga this movement has a range of 90° between positions where the claws point directly posteriorly and directly medially. 50° of this movement is produced, in the normal mammalian fashion, by the radius rotating round the ulna and carrying the hand with it - the cuneiform spins on the ulna at the same time. The other 40° of axial rotation is produced between the carpal bones. The deviational movement at the proximal joint causes some axial rotation, for the unciform slides somewhat extensad and radiad on the cuneiform, while the scaphoid and lunar slide somewhat flexad and radiad on the radius. The mid-carpal joint is more important in this respect, however, for the spiral movement here produces 30°

of axial rotation; equally, the result can be described as 20° flexion with 10° radial deviation. The trapezium and magnum slide extensad and ulnad along the ridge on the scaphoid, while the unciform slides similarly on the cuneiform.

From the remains available, it is obvious that the carpus of the ground sloths (Scelidotherium and Megatherium) (fig.41, p.132) resembled that of Myrmecophaga very closely in structure, and must have been functionally very similar.

TAMANDUA

This smaller anteater is of considerable interest as it is structurally comparable with the terrestrial Myrmecophaga but modified for an arboreal existence.

Compared with the giant form, the main differences in the carpus of Tamandua concern the flexion-extension surface of the proximal joint and the deviation surface at the mid-carpal joint. The distal surface of the radius is rather flatter in FES, and lacks the prominent distally projecting extensor lip. Additionally, the proximal surfaces of the scaphoid and lunar, instead of being diametrically opposite the distal surfaces, spread onto the extensor surfaces of the bones. At the mid-carpal joint, the proximal surfaces of the trapezoid, magnum and unciform form an almost continuous curve (in RUS) instead of a series of separate curves broken especially extensad by stop facets (fig.42, p.133)

Hyperextension of the carpus attains 80°, and flexion 60°, to give a total range of movement in this plane of 140°. Hyperextension is mainly produced at

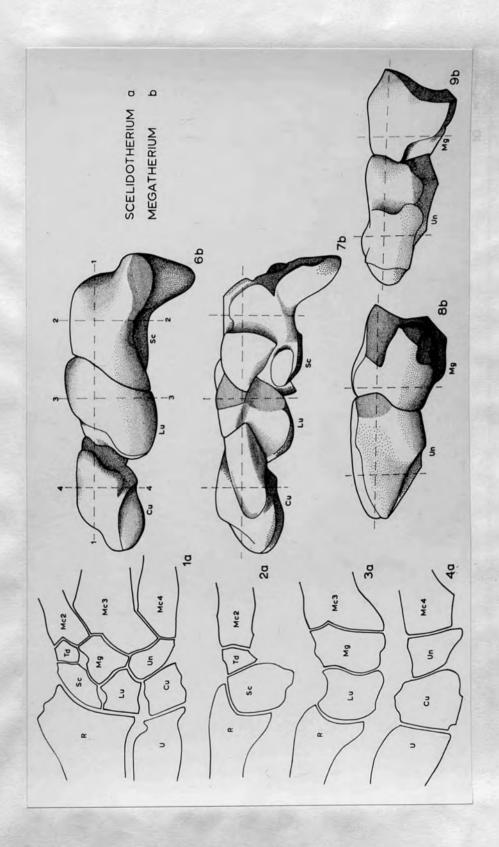


Fig. 41 Partial carpal diagram of Megatheriidae, based on Scelidotherium (a) and Megatherium (b).

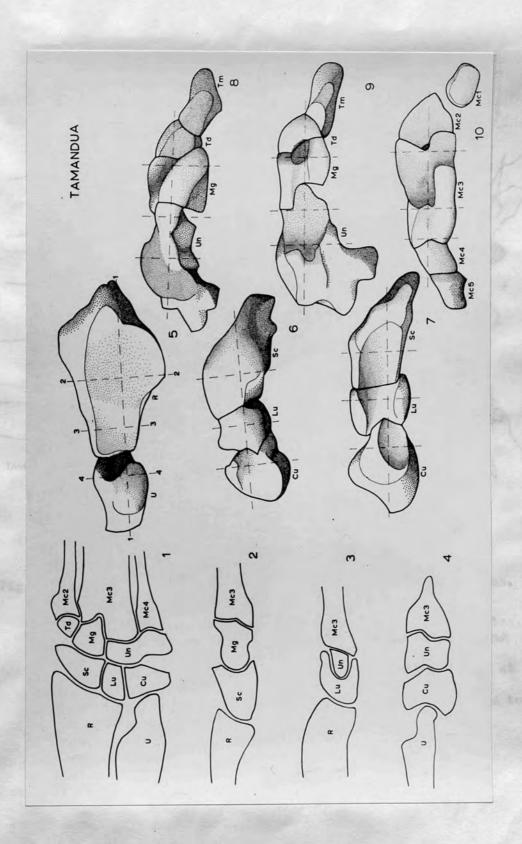


Fig. 42 Carpal diagram of Tamandua.

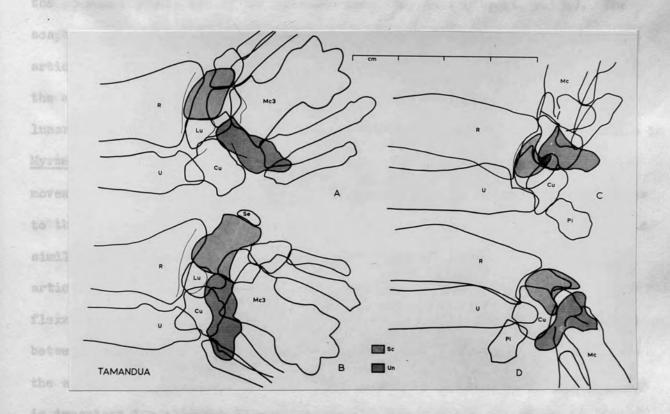


Fig. 43 Action of the carpus of Tamandua, drawn from radiographs.

A Extensor view, in radial deviation.

not part from the bunar in winer devision.

- B Extensor view, in ulnar deviation. As in the primates, considerable movement is evident at both proximal and mid-carpal joints.
- C Radial view, in hyperextension. This occurs mostly at the proximal joint.
- D Radial view, in flexion. Most of the flexion is due to the mid-carpal joint.

the proximal joint, 60° of the movement occurring here (fig.43, p.134). The scaphoid and lunar slide flexad on the radius, and the cuneiform, which articulates loosely to the ulna, slides extensad. At the mid-carpal joint, the magnum and unciform, presenting convex surfaces (in FES) to the scaphoid, lunar and cuneiform, roll flexad on them. Flexion is rather more limited than in Myrmecophaga, and is produced mostly at the mid-carpal joint. Only 20° of the movement is at the proximal joint, the bones sliding in the opposite directions to their movements in hyperextension. At the mid-carpal joint, the movement is similarly opposite to that in hyperextension, except where the unciform articulates to the deeply concave distal surface of the lunar, it rocks on the flexor lip of the cup, thus parting from the lunar extensad; the articulation between the two is a loose fit which allows this movement. It is evident that the absence in Tamandua of the extensor lip of the radius found in Myrmecophaga is important for allowing hyperextension and for limiting the amount of flexion possible.

Deviation involves both proximal and distal joints; both these are a generally concare concave proximal bone surface and a convex distal surface. The possible range of movement is from 40° radial to 30° ulnar deviation. During radial deviation, 20° of movement occurs at the proximal joint, and 20° at the mid-carpal, the rows of bones sliding ulnad at each joint. In radial deviation, rather more of the movement, 20°, is produced mid-carpally, 10° proximally; the movements are the converse of radial deviation. It may be noted that the cuneiform slides ulnad or radial across the ulna, and does not part from the lunar in ulnar deviation.

CHOLOEPUS

The tree sloths, like <u>Tamandua</u>, have a wrist joint of extremely wide manouverability. In <u>Choloepus</u> the radius has a concave distal surface, as seen in both FES and RUS (fig.44, p.137), and the lunar and scaphoid have approximately convex proximal surfaces. The styloid process of the ulna does not project so far distally as the adjoining edge of the radius, and provides a much smaller, slightly convex, articular surface. This adjoins the cuneiform, which is rather cuboidal in section. The proximal surface of the unciform is convex in RUS, almost as curved as the proximal surface of the scaphoid and lunar, though around a different centre of curvature. The rest of the mid-carpal joint is rather irregular. One other important feature of the carpus, though not part of the articulations, is the presence of prominent flexor hooks or tubercles on the scaphoid and on metacarpal 2 (this latter hook probably representing part of the trapezium, which is not present as a separate bone).

The functional proximal joint is between the radius and cuneiform proximally, the scaphoid, lunar and unciform distally; the cuneiform is virtually an extension of the ulna (fig. 46, p. 141). Hyperextension reaches 60°, flexion 40°, and nearly all of this movement is produced at this proximal joint. Hyperextension is produced entirely at this joint, the scaphoid and lunar sliding flexad on the radius so far that the lunar almost disappears from view on the extensor surface of the carpus. The unciform moves with the lunar, passing the cuneiform and causing it to rock into a radially deviated position.

About 20° of the flexion is produced at the proximal joint as well, but the tubercle of the scaphoid meets the radial border of the radius. The tubercle slides inside the border to some extent, causing the scaphoid to

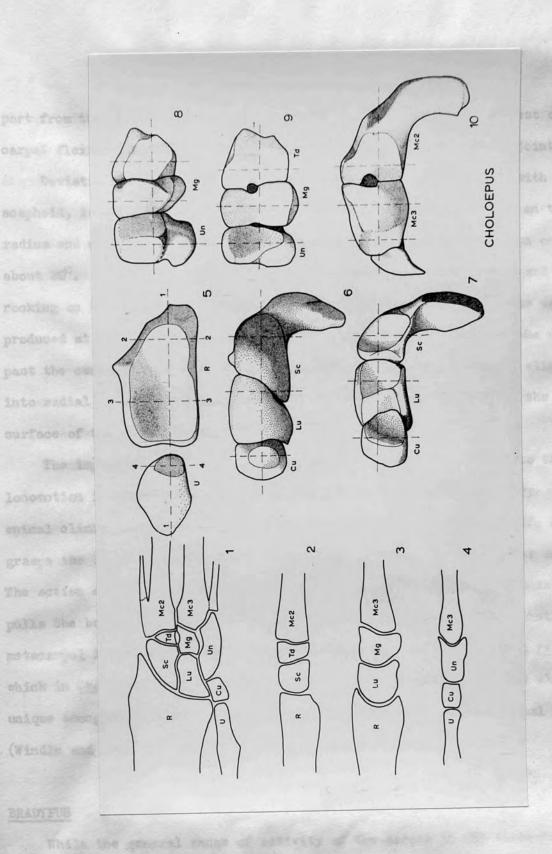


Fig. 44 Carpal diagram of Choloepus.

part from the lunar extensad, but prevents further flexion. The rest of the carpal flexion is produced at the mid-carpal and carpo-metacarpal joints.

Deviation is also a product primarily of the proximal joint, with the scaphoid, lunar and unciform sliding appropriately radiad or ulnad on the radius and cuneiform. Ulnar deviation reaches 50°, radial deviation only about 20°. About 10° of ulnar deviation is produced by the magnum and trapezoid rocking on the lunar and scaphoid, the rest of deviational movements are produced at the proximal joint. The considerable radiad slide of the unciform past the cuneiform in ulnar deviation causes the cuneiform to rock slightly into radial deviation to compensate for the irregular curvature of the proximal surface of the unciform.

The importance of the considerable amount of ulnar deviation to the locomotion is shown by Muybridge's (1957 pl. 145) photographic study. As the animal climbs along beneath a branch, it reaches out ahead of itself, and grasps the branch with the fingers while the wrist is in acute ulnar deviation. The action of (presumably) the <u>flexor</u> and <u>extensor carpi radialis</u> muscles then pulls the body up to the hand. The strong flexor hooks on the scaphoid and metacarpal 2 presumably provide extra leverage for the <u>flexor carpi radialis</u> which in <u>Choloepus</u> inserts to both these bones (in this respect the sloths are unique among mammals as the muscle usually inserts only to metacarpal 2) (Windle and Parsons, 1899).

BRADYPUS

While the general range of activity of the carpus in the three-toed sloths resembles that in the two-toed species, the form of the carpus, and therefore

the method of producing the movements, shows some interesting differences.

The ulna in <u>Bradypus</u> is larger than in <u>Choloepus</u>, projects as far distally as the radius, and forms part of a continuous concave surface with that bone (see fig. 45, p. 140). Correlated with this, the cuneiform is a rather larger bone, convex proximally, forming part of a functional proximal row. The form of the mid-carpal joint is also a concave surface proximally (the distal surface of the scaphoid, lunar and cuneiform) and a convex surface distally (the proximal surface of the magnum and unciform) thus providing another deviational hinge (see RUS). However, the convexity is confined to the flexor half of the magnum and unciform, and forms a curved ridge as shown in the surface view, from radiad to ulnad.

Flexion seems rather more limited than in Choloepus. At the proximal joint, the possible range of movement produced is from 20° flexion to 40° hyperextension. The curved form of the ridge at the mid-carpal joint allows a further 20° of flexion which is combined, however, with 20° radial deviation. The proximal joint provides rather more deviation, from 30° ulnar deviation to 10° radial deviation. In all these movements at the proximal joint, the cuneiform slides with the scaphoid and lunar.

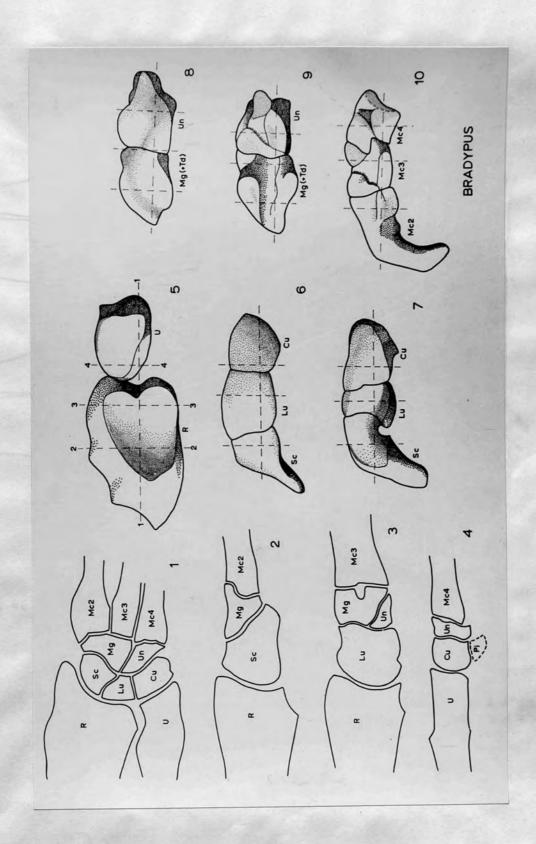


Fig. 45 Carpal diagram of Bradypus.

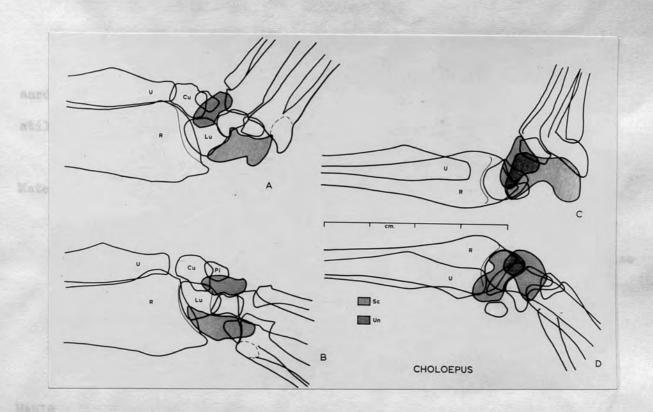


Fig. 46 Action of the carpus of Choloepus, drawn from radiographs.

morphology and confirmally experied to of a time parently to the accident

- A Extensor view, in ulnar deviation.
- B Extensor view, in radial deviation. The unciform moves with the scaphoid and lunar forming a convex proximal joint surface at which almost all deviational movement is produced.
- C Radial view, in hyperextension.
- D Radial view, in flexion. Nearly all of the movement in this plane is produced at the same joint surface, but there is also some movement of the scaphoid past the lunar.

PHOLIDOTA and TUBULIDENTATA

Although it is generally agreed (Simpson 1945) that the pangolins and aardvarks are not especially related to the xenarthran edentates, they may still be congoniently considered next.

Material:

Manis (Smutsia) gigantea - giant pangolin - skeletal BM(N.H.) 1458a and
an un-numbered specimen, also
a fresh-dead specimen

Orycteropus afer - aardvark - skeletal only BM (N.H.)

1948-5-21-1

MANIS

The pangolins are another group of "anteating" (termite-eating) mammals, and resemble Priodontes and Myrmecophaga in having enlarged claws on the digits of the hand which are normally carried flexed. Like those animals, the pangolins walk on the "backs", that is the extensor surfaces, of these enlarged claws. They further resemble Priodontes in having heavy hindquarters and tending to bipedalism. With the forelimbs little used for support, and taking a very short stride the carpus is not so important as a flexion hinge, since the hand does not have to be folded up to clear the ground. The relative immobility of the carpus in this direction is evident from its morphology and confirmed by observation of a live pangolin in the collection of the Zoological Society of London.

The carpus of the pangolin is distinctive among these "anteating" forms in possessing a scapholunar bone. This is a shallowly curved, saucer-like, bone, convex proximally and concave distally, which however bears a large tubercle at the radio-flexor corner (fig. 47, page 144). The proximal articular surface extends onto this tubercle, and is somewhat reflected proximally, to give a groove along this corner of the scapholunar, and a lip which overlaps the equivalent corner of the radius. The radius, therefore, has a rounded, convex, border at this point to an otherwise gently concave distal surface. The distal surface of the ulna is gently convex, but the proximal, concave surface of the cuneiform does not fit tightly to it. The mid-carpal joint closely resembles the proximal joint in general form. The proximal surface of the trapezoid, magnum and unciform forms a gently convex surface opposing the distal concavity of the scapholunar, and the trapezium overhangs the radial border of the scapholunar, in much the same way that the latter bone overhangs the radius.

The shallowness of the curvature of these joint surfaces limits the total range of movements in the flexion-extension range and in deviation. In the normal walking position, the wrist is held in 45° of hyper-extension, and the full flexion movement is 85°, to a 40° flexed position. 50° of this movement is produced at the proximal joint, with the scapholunar sliding extensad on the radius, and the other 35° is produced at the mid-carpal joint by the distal bones sliding similarly on the proximal row. Deviation as such is also rather limited, attaining 10° ulnar and 20° radial deviation; the movement is shared between the two joints.

The most important movement of the carpus, however, is apparently axial

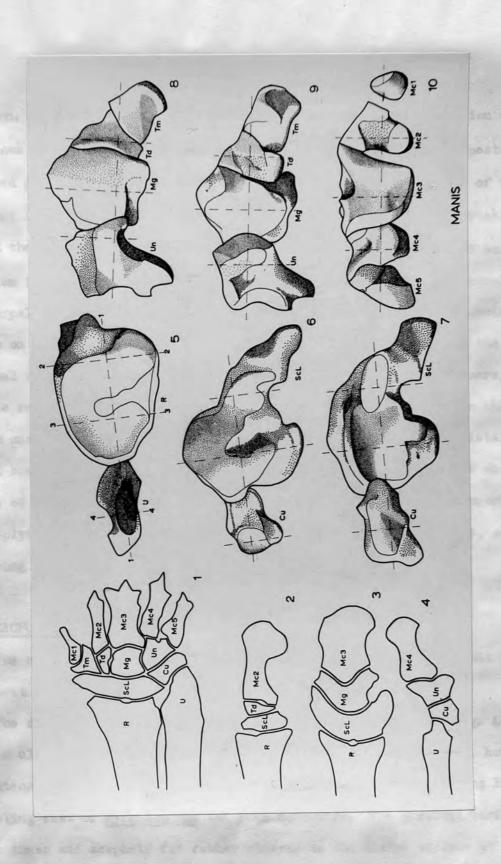


Fig. 47 Carpal diagram of Manis.

rotation. The full extent of axial rotation is 110°, from a position where the claws point 60° medially of directly posteriorly, through the posteriorly directed position, to a position pointing 50° laterally. Some 50° of this movement is produced in the usual mammalian manner by the radius rotating around the ulna, and carrying the carpus with it. The other 60° of axial rotation is a genuine carpal movement, produced equally at the proximal and mid-carpal joints. The scapholunar slides on the radius, as the cuneiform pivots on the ulna, and the distal carpal bones similarly slide on the proximal row. The overall effect is rather of a pile of three saucers, the top one rotating on the middle one, while the middle one rotates on the bottom one. The overlapping radial margins of both proximal and distal radial bones controls the movement, as the overlap slides round the underlying margin of the adjoining bone. This axial rotation is presumably important for applying the claws to the ground for digging into termite hills, and burrowing generally.

ORYCTEROPUS

The carpus of the aardvark has a strange form which is difficult to interpret satisfactorily in the absence of fresh dead material.

The distal surface of the radius is gently concave in RUS (fig. 48, page 147) and the ulna conforms to this plane of curvature. As shown in FES, however, the extensor margin of the radius is distally produced into a strong lip, resembling that of Myrmecophaga but more extensive. The proximal surfaces of the lunar and scaphoid fit rather closely to the distal surface of the radius, and the lunar projects flexad, instead of having a rounded convex flexion facet (as in Myrmecophaga). The mid-carpal joint does not exist as such, since the bones of the proximal and distal rows adjoin along a

rather irregular line.

With this somewhat unusual and angular morphology, it is not surprising that the possible range of movement at the carpus seems to be very slight. Only about 10° of flexion seems possible at the carpus, this produced at the proximal joint by slight movements of the scaphoid and lunar. Deviation, to about 15° ulnar deviation from a straight position, is also produced at the proximal joint, with the scaphoid and lunar sliding radiad across the distal surface of the radius, and the cuneiform moving similarly across the ulnar (fig.49, p.148). In fact the straight position is probably radially deviated from the usual resting position, as the lunar has to move considerably past the ulnar border of the radius, exposing its proximal articular surface, to reach the straight position.

One movement which the carpus of Orycteropus does seem to produce is spreading of the metacarpals. For this, each part of the distal row and the metacarpals it carries moves as a unit on the neighbouring carpal bone (fig. 49, p. 148). Thus the trapezium and trapezoid, carrying metacarpal two slide ulnad on the scaphoid, abducting metacarpal two from metacarpal three through 12°, and the scaphoid can slide further ulnad on the radius and lunar, carrying all the bones distal to it through a further 8°. The magnum, bearing metacarpal three, can slide radiad on the lunar and scaphoid, giving a further 10° abduction, and the unciform, with metacarpals four and five, slides similarly on the lunar to give a further 10° abduction. The net effect of this is to spread the metacarpals from a position where the long axes of the outer ones converge 10°, to a divergence of 30°. Presumably this ability is important in digging, converting the hand from a narrow pick to a wider shovel.

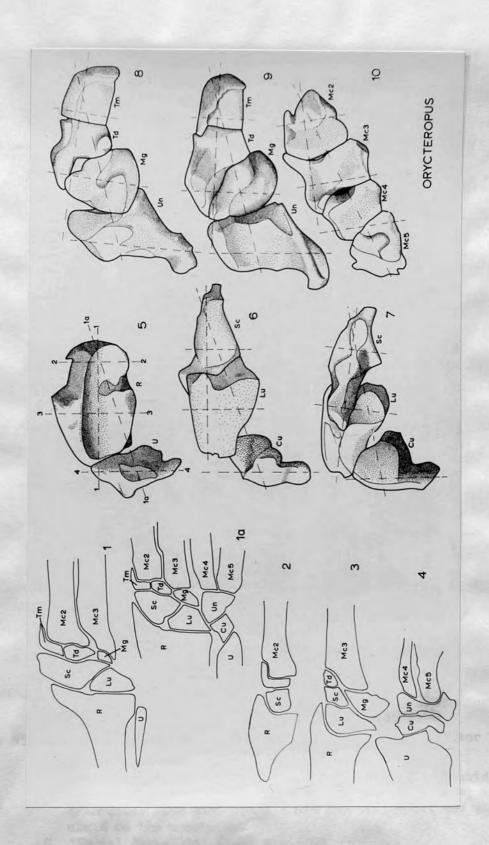


Fig. 48 Carpal diagram of Orycteropus.

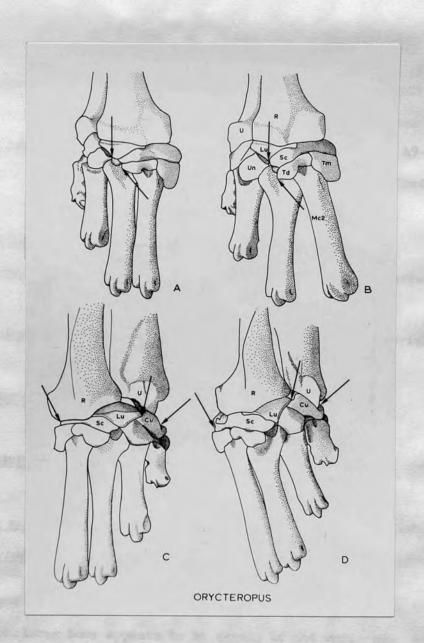


Fig. 49 Action of the carpus of Orycteropus, drawn from extensor view.

A Metacarpals adducted (convergent).

B Metacarpals abducted (spread). Note that the scaphoid and unciform have moved towards each other on the lunar; and the trapezoid, with metacarpal 2 and the trapezium, has moved ulnad on the scaphoid.

C 'Radial deviation' (i.e. straight).

D Ulnar deviation. The proximal row has moved radiad across the radius and ulnar.

RODENTIA

Material:

Castor canadensis - beaver - skeletal BM (NH) 49-7-18-2
and 875e., also fresh dead
specimen.

Sciurus carolinensis - grey squirrel - fresh dead.

Rattus norvegicus - rat - fresh dead and serial sections.

Cavia porcellus - guinea pig - fresh dead and serial sections.

Myocastor coypus - coypu - fresh dead.

Hydrochoerus sp. - capybara - skeletal, BM (NH) 1963-12-10-1
and 1963-8-12-1

Hystrix sp. - porcupine - skeletal BM (NH) 1858-5-26-6

Pedetes caffer - springhaas skeletal BM (NH) 1903-1-4-64

The carpus in the different rodents conforms fairly closely to a common plan. A scapholunar bone appears to be usual, if not universal, and was present in all the forms examined. A distinct centrale is also usual, but is not present in Hystrix, and is of variable size in other forms. The proximal surface of the scapholunar is convex in both RUS and FES, matching the concave distal surface of the radius (see Castor, fig. 50, p.151). As in carnivores, there is a tubercle developed at the flexo-radial corner of the scapholunar which overlaps the flexor margin of the radius. The cuneiform has a concave proximal surface, which fits loosely over the

as well as a flexion hinge, with the cuneiform and scapholunar providing a concave distal surface in RUS, for the convex proximal surface of the distal row. The centrale contributes to this convex surface. The proximal surface of the unciform has the curved, convex surface limited to the more radial side of the bone, the ulnar side being a flat surface which in ulnar deviation closes up to a similar flat on the cuneiform.

CASTOR

The carpus in the beaver (fig. 50, p.151) is particularly interesting in that it allows 100° of hyperextension, so that the forefoot is truly plantigrade. This movement is made possible in the expected manner by the proximal articular surface of the scapholunar extending over and completely occupying the extensor surface of the bone. The extensor margin of the distal surface of the radius is cut back to facilitate this extreme hyperextension, though the movement is still limited by the extensor lip of the radius meeting the centrale. As the scapholunar slides flexad below the radius, so the cuneiform slides extensad round the styloid process of the ulna, and this movement adds some slight radial deviation (10°) to the hyperextension.

The centrale is pushed extensed from between the scapholunar and the distal row, so that the magnum and trapezoid are slightly hyperextended on the centrale. Flexion, to about 70°, occurs likewise at the proximal joint, the scapholunar rocking on the flexor margin of the radius as in carnivores (fig. 51, p. 152). The cuneiform cannot flex so far on the ulna as the

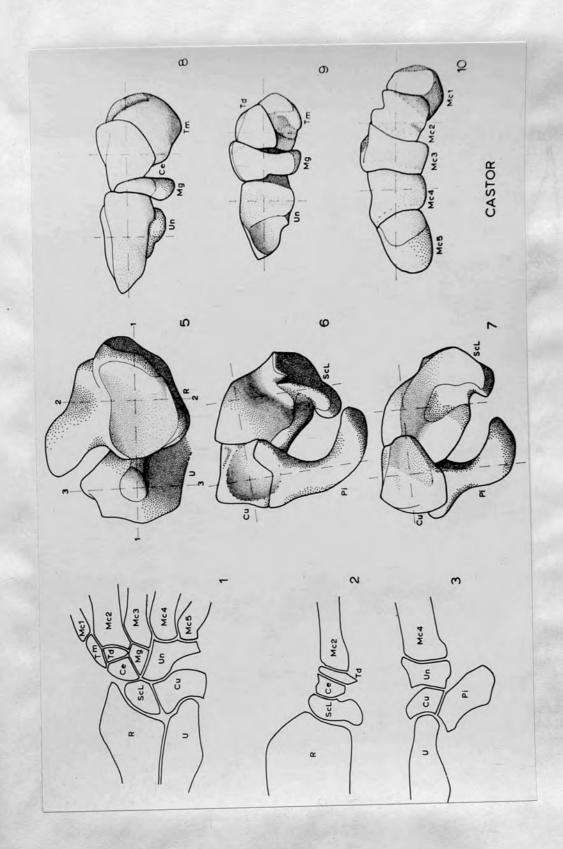


Fig. 50 Carpal diagram of Castor.

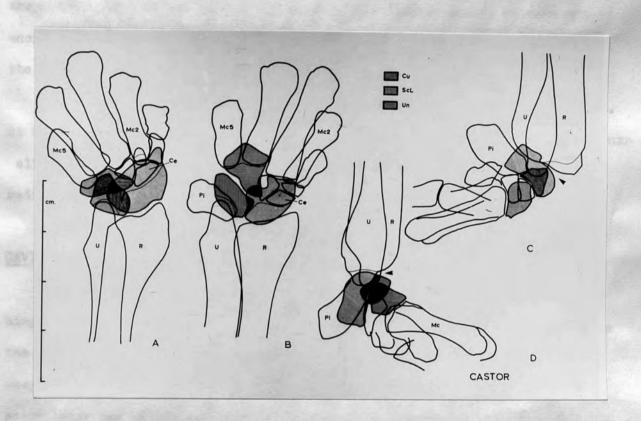


Fig. 51 Action of the carpus of Castor, drawn from radiographs.

- A Extensor view, ulnar deviation.
- B Extensor view, radial deviation. Most of the movement has occurred at the mid-carpal joint, notice especially the position at which the unciform, magnum and centrale converge on the scapholunar.
- C Radial view, flexion.
- D Radial view, hyperextension. Most of the movement occurs at the proximal joint. In flexion, the body of the scapholunar is widely parted from the radius, as in carnivores. In hyperextension, the scapholunar articulates to the radius by its extensor surface, which is continuous with its proximal surface.

scapholunar does on the radius, and some 30° of flexion occurs between the unciform, carried with the rest of the distal row on the scapholunar, and the cuneiform.

Deviation is produced by movement at both proximal and mid-carpal joints.

At the proximal joint, some 10° of radial deviation is possible, the scapholunar sliding ulnad on the radius. The mid-carpal joint can add affurther 10° radial deviation, or give 10° ulnar deviation.

CAVIA

The carpus of the guinea-pig (fig. 52, p. 154) is more strictly a flexion hinge by comparison with the other rodents. This is particularly reflected in the shape of the distal surface of the radius and the opposing surface of the scapholunar. The radius has a deep groove running extensed to flexad, and the scapholunar has an angular proximal surface (as seen in RUS) fitting into it. The weight bearing position of the limb involves 30° hyperextension at the wrist, and full flexion from this position, to 110° flexion, involves movement through 140°. 30° of this movement is produced at the mid-carpal joint, the rest at the proximal joint. At the mid-carpal joint, the distal carpal bones, including the centrale, slide extensed on the proximal row, while at the proximal joint, the cuneiform slides on the ulna, and the scapholunar rocks on the flexor lip of the radius, remaining in contact with the radius only at the base of the tubercle. The slight amount of ulnar deviation possible (10°) is also produced at the mid-carpal joint.

The carpus of the other rodents does not differ especially in function from these two types. Hyperextension is not as extreme as in <u>Castor</u>, deviation

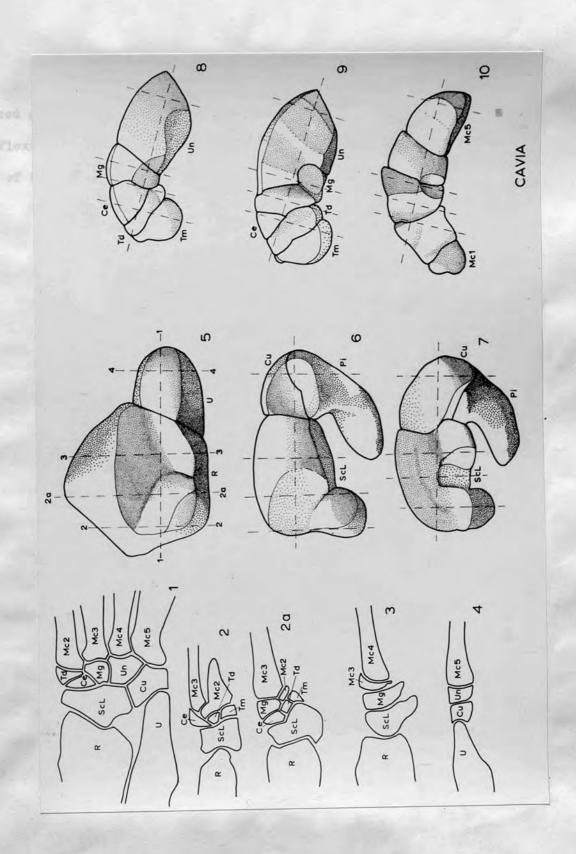


Fig. 52 Carpal diagram of Cavia.

is produced at both proximal and distal joints in most forms, unlike <u>Cavia</u>. In all, flexion at the proximal joint involves the scapholunar rocking at the base of the tubercle on the flexor lip of the radius.

Lapus europeeus - have - fresh dead

The carpus of the lagomorphs differs from that of the rodents in having the three bones of the proximal row separate. The centrals is distinct. The proximal joint has a rather irregular surface so esen in RUS, (fig. 53. p. 157) as the radius has separate concave surfaces for the scaphoid and lanar, and the ulma is as usual convex. The surfaces of the radius and ulma show the same shape in FES. The mid-darpal joint is even more irregular in RUS than the proximal joint; in FES the trapezium and the unciform with metacarpal 5 bear convex proximal surfaces toward the flower side which articulate to the scapholumar and the conciform respectively (metacarpal 5 projects proximally past the unciform).

Plexion reaches 140°, of which 100° is produced at the proximal joint. The scaphoid rocks on the flavor lip of the radius, and the cureifors alides flexed round the wine. This is an oblique hinge, however, seems the wine projects further distally than the radius, and the lawer is lifted where of the radius in full flaxion by the movements of the bases either aids of it. The movement at the mid-carpal joint is similar. The movement at the mid-carpal joint is similar. The magnetic flaxes on the scaphoid, sliding extensed, and materiary of flaxes countries as lifted clear of the proximal row in full flaxion. Some alight deviation is prescribe, assenting only to 10° where deviation, and this is also produced at the mid-carpal joint of the proximal row in full flaxion. Some alight deviation is prescribe, assenting

LAGOMORPHA

Material:

Lepus europaeus - hare - fresh dead

The carpus of the lagomorphs differs from that of the rodents in having the three bones of the proximal row separate. The centrale is distinct. The proximal joint has a rather irregular surface as seen in RUS, (fig.53, p.157) as the radius has separate concave surfaces for the scaphoid and lunar, and the ulna is as usual convex. The surfaces of the radius and ulna show the same shape in FES. The mid-carpal joint is even more irregular in RUS than the proximal joint; in FES the trapezium and the unciform with metacarpal 5 bear convex proximal surfaces toward the flexor side which articulate to the scapholunar and the cuneiform respectively (metacarpal 5 projects proximally past the unciform).

Flexion reaches 140°, of which 100° is produced at the proximal joint. The scaphoid rocks on the flexor lip of the radius, and the cuneiform slides flexad round the ulna. This is an oblique hinge, however, because the ulna projects further distally than the radius, and the lunar is lifted clear of the radius in full flexion by the movements of the bones either side of it. The movement at the mid-carpal joint is similar. The trapezium flexes on the scaphoid, sliding extensad, and metacarpal 5 flexes similarly on the cuneiform, so that the trapezoid, centrale, magnum and unciform are lifted clear of the proximal row in full flexion. Some slight deviation is possible, amounting only to 10° ulnar deviation, and this is also produced at the mid-carpal joint.

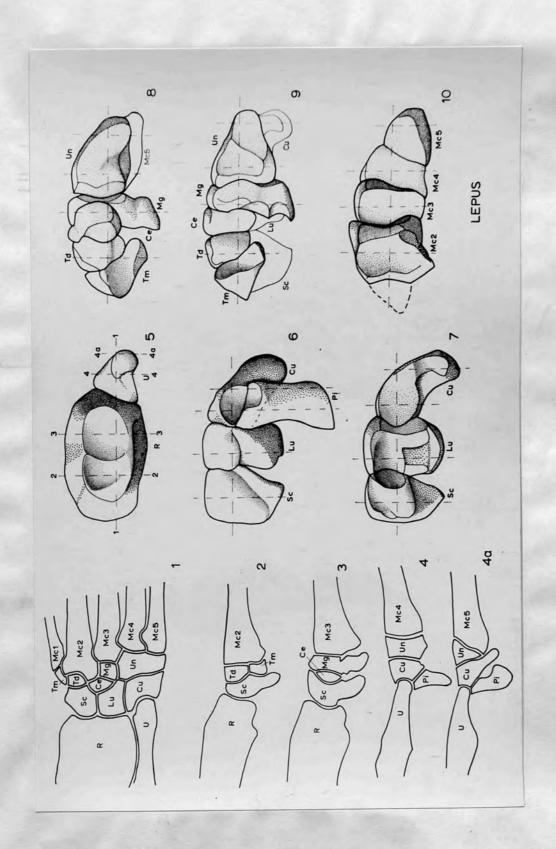


Fig. 53 Carpal diagram of Lepus.

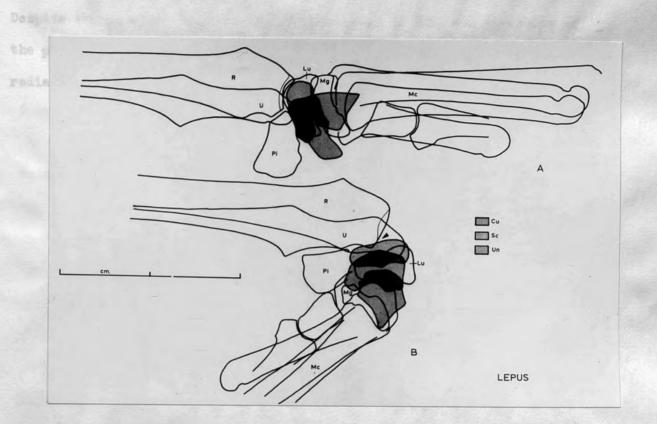


Fig. 54 Action of the carpus of Lepus, drawn from radiographs.

- A Radial view, carpus extended.
- B Radial view, carpus flexed. In flexion, the scaphoid and lunar are widely parted from the radius, the lunar completely so, the scaphoid rocking on the flexor lip of the radius.

Despite the apparent irregularity of this joint in RUS, the curvature of the proximal surfaces of the distal carpal bones allows them to slide slightly radiad on the proximal bones.

Simpson 1945), the carpi in different insectivores differ considerably.

Materials

Eximencus europeanus - hedgehog - skeletal and fresh dead

Rayndhodyon cernsi - elephant naraw - skelatal only

Petrodromus sultan - elephant shrew - preserved specimen

Tupela minor - tree shrew - skeletal only

ERINACEUS and BERRY

The carpus in these two forms is quite similar. There is a scepholunar bone, which probably includes the fused scapheid, lunar and centrale,
as in carniveres, though this is not certainly established by the
embryological studies of Hologren (1952). Certainly the scaphoid and
lunar are parts of the bone, but the fate of the centrale seems to be less
clear. The proximal joint in these two forms resembles that in the carniveres
and recents, with the scaphelimer scarax proximally (in both RUS and FES)
for the radius, and the sumelform conduce for the ulna (fig.55, p.161). The
styloid process of the ulna is rather elongate in RUS. The mid-carpal joint
is rather irregular in RUS (like the carniveres, but unlike the redents), but
the proximal surfaces of the distal carpal beness are contex in FES, opposing
generally occurve distal surfaces on the scapholunar and constitute.

INSECTIVORA

As might be expected in a group which is of disputed homogeneity (see Simpson 1945), the carpi in different insectivores differ considerably.

Material:

Erinaceus europaeus - hedgehog - skeletal and fresh dead

Sorex araneus - common shrew - fresh dead

Rhynchocyon cernei - elephant shrew - skeletal only

Petrodromus sultan - elephant shrew - preserved specimen

Tupaia minor - tree shrew - skeletal only
Talpa europaea - mole - fresh dead

ERINACEUS and SOREX

The carpus in these two forms is quite similar. There is a scapholunar bone, which probably includes the fused scaphoid, lunar and centrale, as in carnivores, though this is not certainly established by the embryological studies of Holmgren (1952). Certainly the scaphoid and lunar are parts of the bone, but the fate of the centrale seems to be less clear. The proximal joint in these two forms resembles that in the carnivores and rodents, with the scapholunar convex proximally (in both RUS and FES) for the radius, and the cuneiform concave for the ulna (fig.55, p.161). The styloid process of the ulna is rather elongate in RUS. The mid-carpal joint is rather irregular in RUS (like the carnivores, but unlike the rodents), but the proximal surfaces of the distal carpal bones are convex in FES, opposing generally concave distal surfaces on the scapholunar and cuneiform.

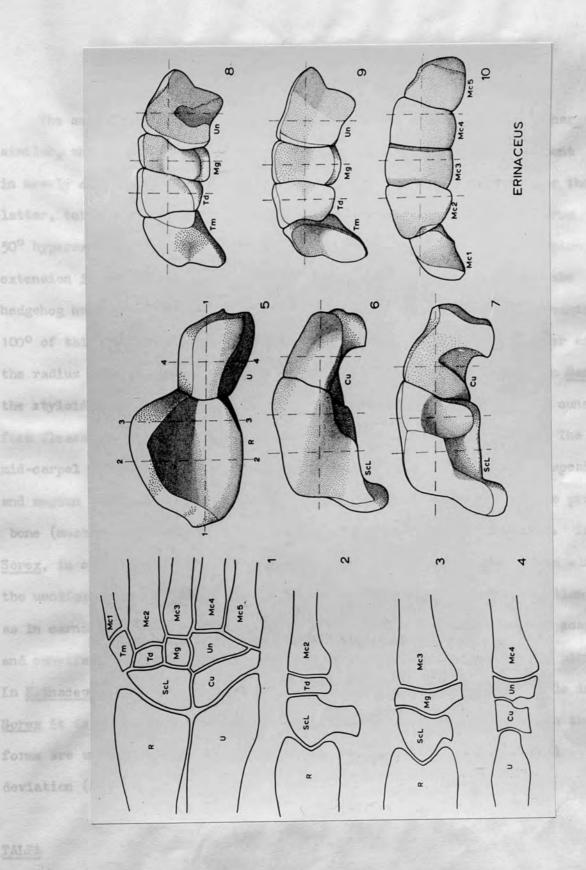


Fig. 55 Carpal diagram of Erinaceus.

The amounts of movement produced in both these forms are also rather similar, though the carpus of Sorex seems to allow slightly more movement in nearly all directions than that of Erinaceus. Using the figures for the latter, total movement in the flexion-extension plane is about 1700, from 50° hyperextension to 120° flexion (as with Ursus q.v. p.51) 50° hyperextension is not sufficient to allow a plantigrade limb position, and the hedgehog has an essentially digitgrade forelimb). The proximal joint contributes 100° of this movement, with the scapholunar rocking on the flexor border of the radius and the cuneiform sliding flexad on the ulna in flexion. In Sorex the styloid process of the ulna forms a distinct condyle, on which the cuneiform flexes 130°, 30° more than the scapholunar flexes on the radius. The mid-carpal joint contributes a further 70° of flexion, in which the trapezium and magnum slide on the scapholunar, lifting the trapezoid clear of the proximal bone (much as in carnivores) and the unciform flexes on the cuneiform. In Sorex, in correlation with the greater movement of the cuneiform on the ulna, the unciform only flexes 40° on the cuneiform (fig. 56, p. 163). Deviation, as in carnivores, is produced entirely at the proximal joint, with the scapholunar and cuneiform sliding ulnad or radiad as appropriate on the radius and ulna. In Erinaceus, the range is from 20° radial to 15° ulnar deviation, while in Sorex it is possible to obtain 30° radial or 10° ulnar deviation. Both these forms are unusual among mammals in possessing greater freedom of radial deviation (fig. 57, p. 164).

TALPA

Reed, in his thorough analysis of specialisations in the limbs of talpids

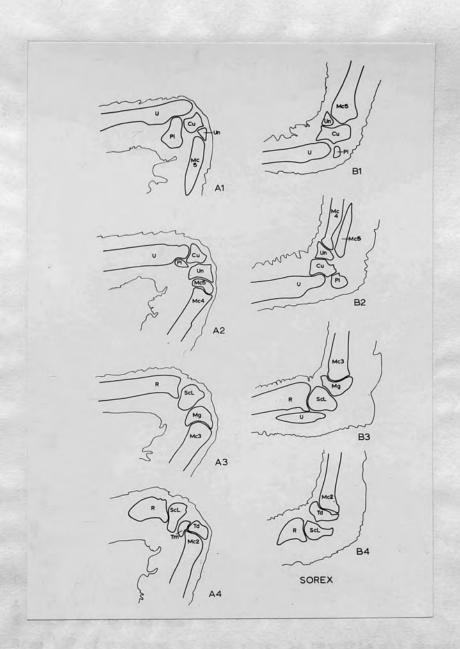


Fig. 56 Carpus of Sorex in FES, drawn from serial sections.

A 1-4, in flexion. B 1-4, in hyperextension.

The range of movement is from 600 hyperextension to 1350 flexion, most of which occurs at the proximal joint. The cuneiform slides flexad round the ulna through 130°. The scapholunar flexes 100° on the radius, rocking on the flexor lip of the radius and parting from it extensad.

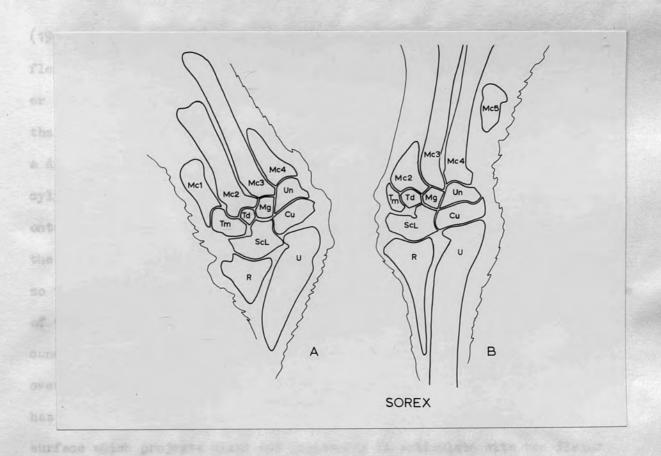


Fig. 57 Carpus of Sorex in RUS, drawn from serial sections.

A in radial deviation.
B in ulnar deviation.

Some 45° of movement in this plane is possible all occurring at the proximal joint. The more distal position of the radius and scapholunar in B is an illusion due to the plane of section.

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(1951) mentions (p. 561) that the wrist is a hinge joint, allowing only flexion and extension but does not investigate the details of the structure or action of the bones. The carpus of the moles is more primitive than that of the shrews in possessing a separate scaphoid and lunar, and also a distinct centrale. The scaphoid and lunar articulate to the radius by cylindrical proximal surfaces, convex in FES (fig. 58, p. 166) which extend onto the extensor surfaces of the bones. As the RUS shows, the surface of the scaphoid is not in line with that of the lunar, but sloped towards it so that together the bones form a gentle groove, for which the distal surface of the radius is appropriately slightly keeled. The proximal surface of the cuneiform has a groove, somewhat elongated from radiad to ulnad, which fits over the similarly elongated, styloid process of the ulna. The cuneiform has a prominent flange developed from the flexor side of the proximal surface which projects ulnad and proximally to articulate with the flexor side of the styloid process of the ulna, at least, in the extended position. As Reed notes, the distal surfaces of the radius and ulna, though parallel, are not in line (fig. 58,5; p. 166) the radius lying more extensad than the ulna. This has some importance in the action of the wrist. One other important feature, not noted by Reed, is the development of a flat flexor surface to the proximal row, to which all three bones contribute. This surface extends considerably in a proximal direction, and carries the great ligament of the flexor digitorum profundus past the carpus. The contribution from each bone is irregular in shape, so that although the three bones are quite distinct, they are tightly bound together, and no movement between them is possible.

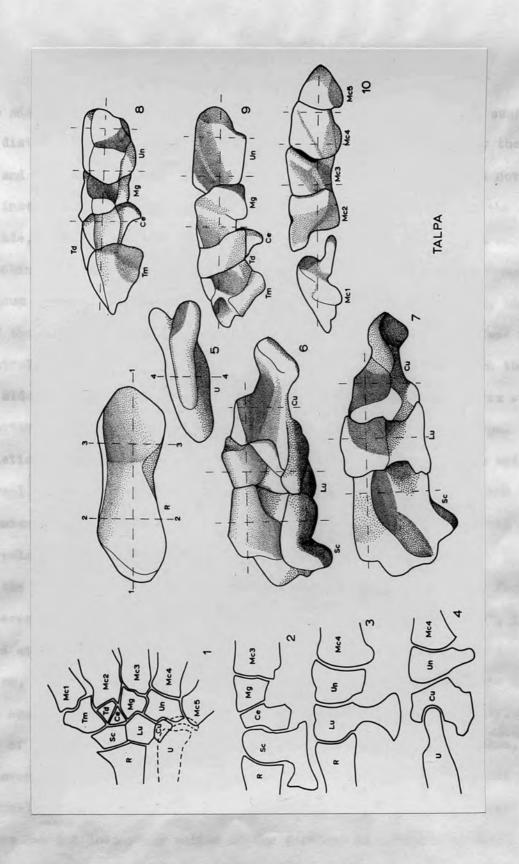


Fig. 58 Carpal diagram of Talpa.

The mid-carpal joint is somewhat irregular. In FES the proximal surfaces of the distal carpal bones all tend to be gently convex, particularly the magnum and unciform. In RUS, though, a mid-carpal joint as such does not exist, instead the articulations are arranged into three joints. On the ulnar side, the unciform articulates to the cuneiform and lunar by an angular, interlocking surface which precludes any movement in this plane. Although the magnum similarly interlocks with the lunar towards the ulnar side, the rest of the proximal surface of the magnum forms a smooth convex surface with the centrale which articulates to the lunar and scaphoid. Finally, on the radial side, the trapezium and trapezoid together form a similar convex surface which articulates to the centrale and scaphoid. Of the carpo-metacarpal articulations, those between the trapezium and metacarpal 1, unciform and metacarapl 4, and unciform and metacarpal 5 are all smooth curves in RUS and allow movement in this plane, but the joints of the magnum and trapezoid with metacarpals 3 and 2 respectively are irregular and interlock.

In the flexion-extension plane, the possible range of movement is from 90° hyperextension to 30° flexion. The majority of this movement, 70°, is produced at the proximal joint (fig. 59, p. 168). From the hyperextended position, the cuneiform slides flexad round the styloid process of the ulna, and the scaphoid and lunar slide extensad on the radius. Since the styloid process of the ulna lies more flexad than the distal surface of the ulna, these movements ought to cause ulnar deviation, as in other mammals, but the cylindrical nature of the joint surfaces in the mole prevents this. Reed describes how the locomotory action of the forelimb is produced by axial rotation, and goes on to show that flexion of the wrist is produced automatically by this rotation of the humerus. If the elbow is viewed from

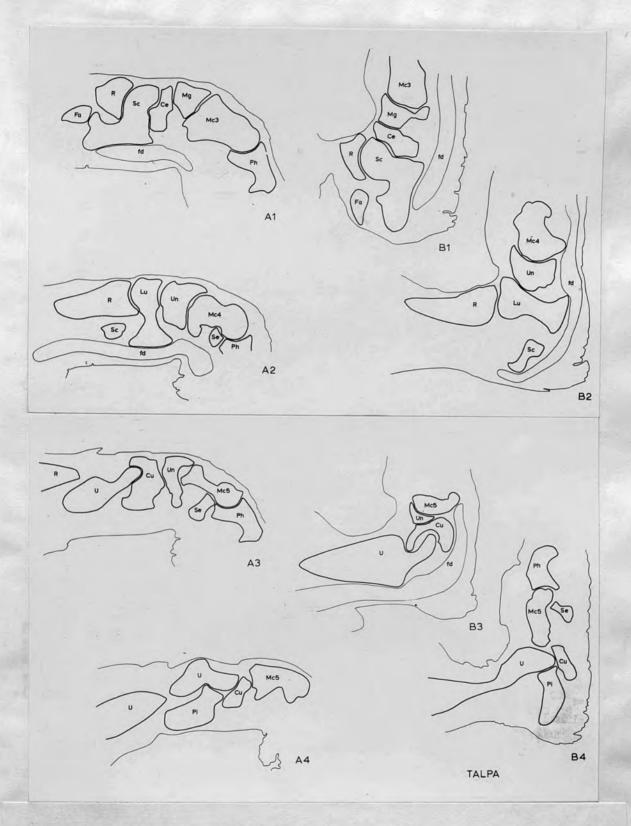


Fig. 59 Carpus of Talpa in FES, drawn from serial sections.

- A in extension
- B in hyperextension

Almost no flexion occurs, but 90° of hyperextension is possible; movement occurs mainly at the proximal joint.

The advantageous leverage gained by the <u>flexor digitorum profundus</u> tendon (f.d.p.) in passing over the flattened projections on the flexor sides of the proximal carpals is shown especially in B 2.

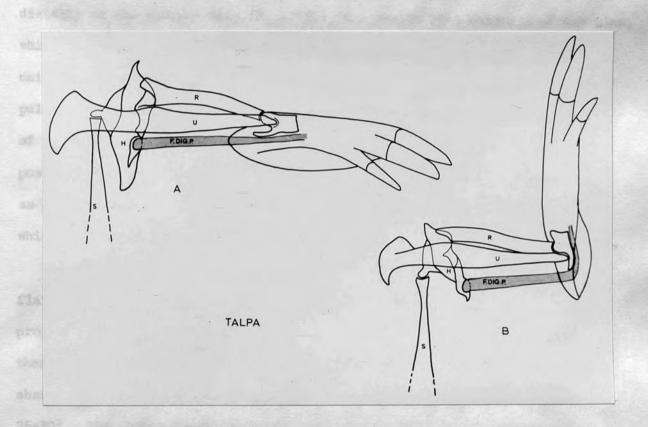


Fig. 60 Action of the forearm in <u>Talpa</u>. From the hyperextended position, B, rotation of the humerus (H) (by the main digging muscles) will pull the tendinous <u>flexor digitorum profundus</u> (F. DIG. P.) and push the radius (R) past the ulna (U), thus extending the carpus, as in A. (S, scapula, lying much deeper).

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distally of the humerus (fig. 60, p. 169), the radius lies extensed of the ulna, while the <u>flexor digitorum</u> tendon lies flexad. These relationships are maintained the full length of the forearm, so that rotation of the humerus pulls this tendon proximally past the ulna, to give the automatic flexion of the wrist. Reed failed to note, however, that this action must also push the radius distally past the ulna, so that the wrist is pushed, as well as pulled, into flexion. It is this sliding of the radius past the ulna which allows the proximal articular surfaces of the carpus to be cylindrical.

One other feature which Reed failed to notice is the rôle played by the flattened flexor extensions of the proximal bones. In hyperextension, these project flexad of the carpus, and, as the <u>flexor digitorum</u> tendon pulls over them, provide an added lever (fig. 59, p. 168). The rest of the flexion is shared between the mid-carpal and carpo-metacarpal joints, each flexing 25-30°. The magnum flexes on the centrale and lunar, since the centrale does not flex on the scaphoid.

Reed failed also to notice the rôle played by the carpus in spreading the hand. This is partly produced by the metacarpo-phalangeal joints, but some 30° of divergence between metacarpals 1 and 5 can be produced at the carpus. Metacarpal 5, sliding on the unciform, can abduct 15° from metacarpal centrale slide on the 4; the magnum and lunar, carrying metacarpal 3 into 5° abduction from metacarpal 4; and the trapezium and trapezoid, sliding on the scaphoid and centrale, abduct metacarpals 1 and 2 through 10° from metacarpal 3.

RHYNCHOCYON

The carpus of Rhynchocyon bears a remarkable resemblance in both form

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and mode of action to that of a horse. At the proximal joint, the radial side of the radius extends distally and flexad, providing a "higher" surface for the scaphoid than the lunar (fig. 61, p. 172). At the mid-carpal joint, the distal surface of the lunar bears a concavity flexad which articulates with a corresponding convexity on the magnum. Although the centrale is a distinct bone, the mid-carpal joint is too irregular, as shown in RUS, to allow deviation; the same is true of the proximal joint. In flexion, the centrale appears to move with the distal carpal row.

<u>PETRODROMUS</u> resembles <u>Rhynchocyon</u> in the general form of its carpus, but would seem to be a less specialised type. The radius is not produced distally for the scaphoid, and deviational movements can be produced at the mid-carpal joint as this is smoother in RUS (fig. 62, p. 173). The centrale moves with the distal carpal bones in deviation, but stays with the proximal row in flexion.

TUPALA

While the carpus of this animal was too small to allow a full analysis, a short account is of some interest in view of the intermediate position members of the Tupaiidae hold between the primates (where they are classified by Simpson 1945) and the insectivores (where, for instance, Evans, 1942, prefers to place them). As far as the carpus is concerned, the scaphoid and lunar are fused into a scapholunar bone (Evans 1942, implies that this is not always so, though Grasse, 1955, Flower 1885; and Gregory 1910, suggest that it is; in the young specimen I examined they were fused). This is

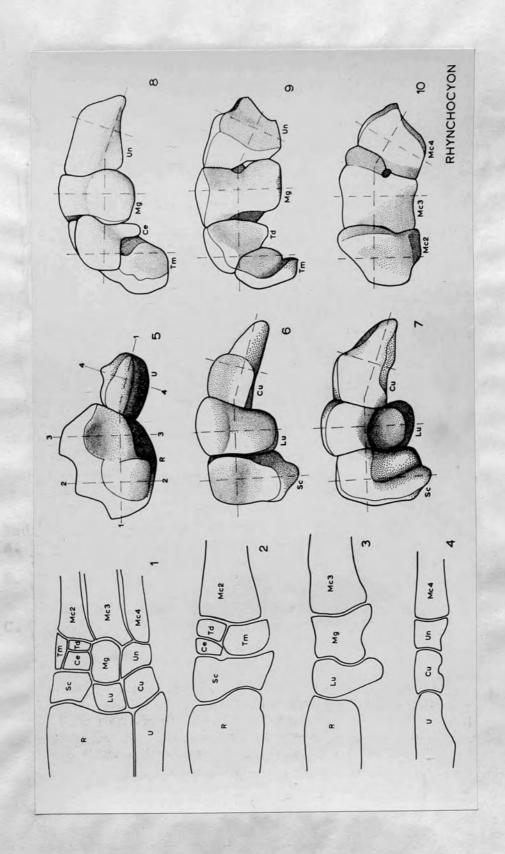


Fig. 61 Carpal diagram of Rhynchocyon.

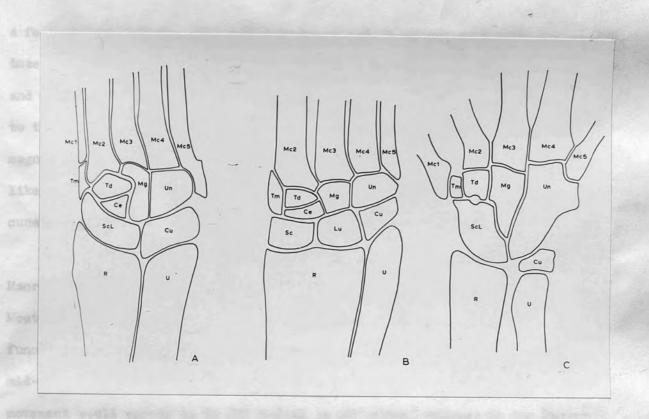


Fig. 62 Radio-ulnar sections through the carpus of :-

past. This is a printive frattee out appearance total to the a

A. Tupaia. The form of t he mid-carpal joint is comparable with that of primates (cf. fig. 36, p.117).

B. Petrodromus. This resembles Rhynchocyon (fig. 61, p.172)

but is less specialised; both proximal and mid-carpal joints are smoother curves.

C. Phascolarctos. Compared with Vombatus, (fig. 68, p.188) this shows the emphasis on producin g deviation seen in

It is interesting to note that all the dramativerse, including Topole,

arboreal mammals.

a feature not found in any primate, though not found either in all insectivores. The centrale is distinct, a feature of many insectivores and primates. Gregory (1910) emphasises the resemblance in general form to the primates, particularly in the nature of the mid-carpal joint. The magnum is rather compressed, as would be shown in RUS, and forms a primate-like joint with the unciform in articulation with a surface formed by the cuneiform, lunar and centrale (fig. 62, p. 173).

Evans (1942) listed several similarities between the carpus of Macrosce tididae and Tupaiidae which he felt indicated a close relationship. Most of these are superficial or primitive characters, however, and the functional patterns seem rather different. In particular, both proximal and mid-carpal joints in Tupaia allow deviational movements (the total range of movement would appear to be 200 radial to 200 ulnar) whereas in the Macroscelididae the proximal joint is solely a flexion hinge. This dual deviational hinge is a primitive character, typical of the primates and found also in most rodents. Of the other insectivores, Petrodromus has a deviational hinge at the mid-carpal joint, like Tupaia, in which the centrale slides with the other distal carpal bones on the proximal row, but the rest cannot produce deviation at this joint. In Tupaia, and also in Petrodromus, the centrale stays with the scaphoid and lunar in flexion, while the distal bones flex past. This is a primitive feature not apparently found in the primates, but the arrangement of the carpals in Tupaia certainly seems to be an intermediate stage in the development of the primate type of arrangement.

It is interesting to note that all the insectivores, including <u>Tupaia</u>, seem to have an elongated styloid process on the ulna (elongated from radially

to ulnad) which as Reed (1951) notes for the Soricoids, would seem to preclude any supination occurring.

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CHIROPTERA

Material:

Megachiroptera;

Pterocyon sp. - flying fox - preserved specimen

Pteropus sp. - flying fox - fresh dead (though diseased) and skeletal

Microchiroptera;

Scotophilus sp. - preserved material

Pipistrellus sp. - preserved material

The carpus in Microchiroptera contains two bones in the proximal row, a cuneiform and a scapholunar which Lebourcq (1884) showed in Vespertilio murinus to be a compound scaphoid, lunar, and centrale. In the Megachiroptera, there is generally only one bone, the cuneiform being presumably fused to the scapholunar. Apart from this distinction however, which appears to be of little functional importance, the carpus of the Chiroptera can be described in one general account. This is primarily based on Megachiroptera because the larger size of the bones facilitates observation.

The carpus of the bats is difficult to describe without first describing the position of the wing in the terms used to describe other mammals. As usually drawn with the wing spread, a bat appears to have the fingers spread in ulnar deviation, but this is illusory. The carpal hinge is aligned as in most mammals in the same plane as the elbow, and the fingers are in fact in various degrees of flexion. Thus, when the wing is spread, (fig. 63, p. 177) metacarpal 2 is flexed 20° relative to the long axis of the radius, and

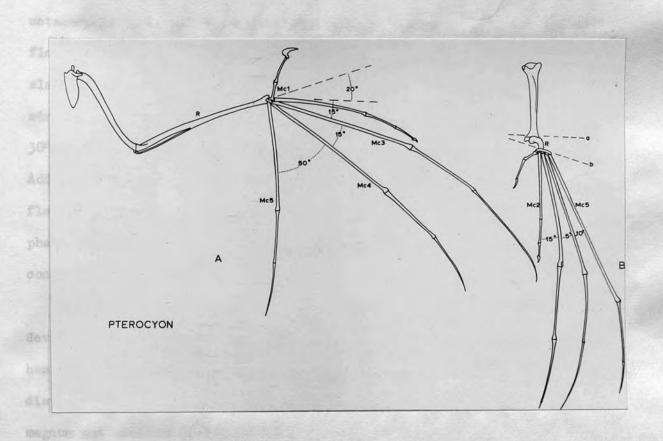


Fig. 63 Position of the metacarpals in the chiropteran wing when spread.

- A Radial view
- B Distal view

Folding the size to an Stat Juneal

Note from A that the spreading of the wing is due to the metacarpal bones being differentially flexed. Hence when the wing is furled, the metacarpals each flex through the angle necessary to give 180° flexion. B shows that the metacarpals are also abducted (spread) from each other, contributing to the aerofoil section (camber) of the wing.

metacarpals 3, 4, and 5 are similarly held in positions 35°, 50° and 100°. flexed respectively. As an additional complication, the metacarpals are also abducted somewhat from each other, so that if metacarpal 2 is in a straight flexion plane metacarpal 3, 4, and 5 are abducted 15°, 20° and 30° from it respectively. This gives the wing an adequate curved chord. Additionally, while the proximal ends of the metacarpals flex in a normal flexion plane, the shafts are twisted so that, the distal ends, the metacarpophalangeal joints flex in a plane at right angles to this, thus also controlling the curvature of the chord.

The proximal and mid-carpal joints are both irregular in RUS, and deviational movements are not possible. In FES, the scapho-lunar-cuneiform has a wedge-shaped proximal surface which fits rather tightly into the notched distal surface of the radius. (fig. 64, p. 179). At the mid-carpal joint, the magnum and unciform provide a convex, semi-cylindrical surface which articulates with, and flexad of, a concave surface on the scapholunar. The trapezoid is concave proximally, and articulates with a distally projecting condyle. The trapezium articulates by a curious, hook-like, proximal process over the extensor side of a distally projecting ledge on the scapholunar. The carpometacarpal articulations are important in bats. As shown in FES, metacarpal 2 articulates to the trapezoid by a rather flat proximal surface which is convex flexad where it meets a radially projecting ledge of the magnum.

Metacarpal 3 is wedge shaped in RUS, a convex wheel in FES, and articulates between the magnum and unciform, while metacarpal 4 is similarly wedged between the unciform and the proximal end of metacarpal 5.

Folding the wing is in fact carpal flexion. The irregular nature of the

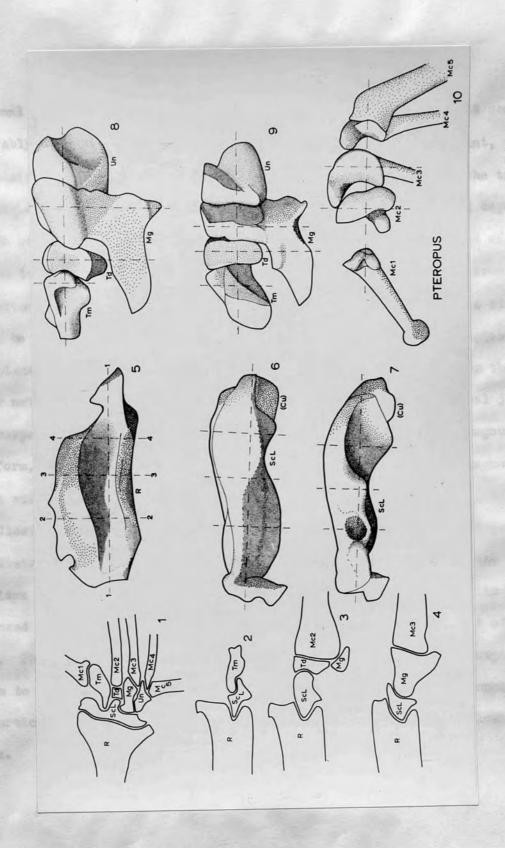


Fig. 64 Carpal diagram of Pteropus.

proximal joint in this plane limits flexion here to about 20°, but considerably more flexion, 80°, can be produced at the midcarpal joint, with the unciform and magnum sliding extensed on the scapholunar and the trapezoid sliding flexad. The amount of flexion required to close the wind depends on the positions of the metacarpals. The 100° of flexion produced at the carpus is sufficient to close metacarpal 5 to the radius, though some 30° adduction (as I have described the position of metacarpal 5; this adduction could be regarded as flexion, but if so is in a plane at right angles to the plane of flexion of the other metacarpals), is required. For the other metacarpals, further flexion is produced at the distal carpal joints. Metacarpals three and four flex 60° and 40° respectively on the magnum and unciform, while metacarpal two, flexing 80° on the ledge of the magnum, parts widely from the trapezoid extensed.

Closing a bat's wing depends then largely on the use of the mid-carpal and distal carpal joints as flexion hinges. The manner in which the radius overlaps the magnum and unciform, presumably helps lock the wrist in the extensad position and prevents hyperextension during the down beat of the wing. The peculiar form of the joint between the trapezium and scapholunar seems to be responsible for most of the manoeuverability of the thumb, as the articulation of the trapezium to metacarpal one is solely a flexion hinge.

DERMOPTERA

Material:

Cynocephalus volans - cobego - skeletal only BM(N.H.) 1877-10-6-4

The cobego is of interest as a form frequently regarded as intermediate between the bats and insectivores. The carpus is too small to allow a full analysis, but some interesting points can be made. As fig. 65, p. 182 shows, there is a scapholunar which has a strongly convex proximal surface articulating to a deep cup on the radius. This allows 80° flexion movement (from 20° hyperextension to 60° flexion) and 40° deviation (10° radial to 30° ulnar). The mid-carpal joint is irregular in RUS, but a hinge in FES allowing 30° flexion, As in bats, the trapezoid is carried and a convex condyle, and is lifted clear of the scapholunar by the flexion of the trapezium and magnum either side of it. Another feature suggestive of the chiropteran carpus is a process on the trapezium which hooks over the extensor surface. This does not form the flexion hinge with the scapholunar but does suggest how the peculiar articulation of this bone in the Chiroptera might have originated.

rig. 65 carrel distres of Cyrocophalus.

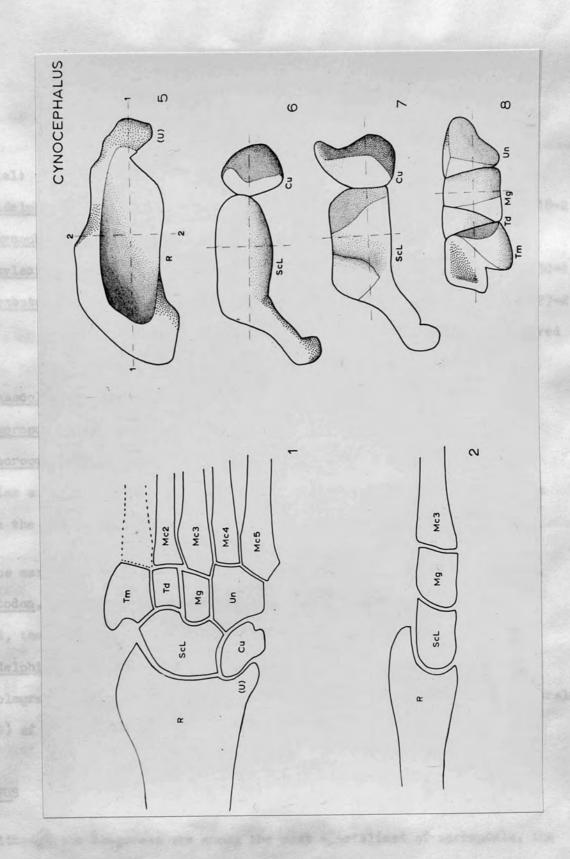


Fig. 65 Carpal diagram of Cynocephalus.

The boundaries to access a MARSUPTALIA

Material:

Didelphis marsupialis - opossum - skeletal BM(N.H.) 1949-1-18-2

Sarcophilus harrisi - tasmanian devil - fresh dead

Thylacinus cynocephalus - tasmanian wolf - skeletal BM(N.H.) 1963-8-30-1

Vombatus sp. - wombat - skeletal BM(N.H.) 1950-3-27-2

and 1496d. Also a preserved

carpus takes place between the maddus and specimen.

Phascolarctos cinerea - koala - skeletal BM(N.H.) 229

Macropus rufus - red kangaroo - fresh dead

Macropus ruficollis - wallaby - fresh dead

Also a cursory examination of a mountd skeleton of Diprotodon australis in the public gallery of the BM(NH).

The marsupial carpus frequently has a scapholunar bone, as in <u>Vombatus</u>,

<u>Diprotodon</u>, <u>Phascolarctos</u> and <u>Macropus</u> of the list above. In the others

listed, the scaphoid and lunar are distinct, though tightly bound together

in <u>Didelphis</u>. A separate centrale is never apparent in adult marsupials,

but Holmgren (1952), describes what is apparently a separate centrale (centrale

3 (+2) of his terminology) in an embryo of <u>Perameles</u>.

MACROPUS

Although the kangaroos are among the most specialised of marsupials, the carpus has a generalised form and may be considered as a conveniently available type.

that mess 50° hypercutenzion is obtainable at the wrist. This is not due,

The scapholunar is convex proximally, with a moderate tubercle, and opposes a concave distal surface on the radius, while the cuneiform is concave proximally and articulates with the condyloid distal end of the ulna. The unciform is a large bone, convex proximally in RUS (fig. 66, p. 185) on the same radius of curvature as the scapholunar, but flattened toward the ulnar side. The more radial side of the unciform has the proximal surface convex also in FES.

As might be expected, the majority of the movement occurring at the carpus takes place between the radius and cuneiform proximally and the scapholunar and unciform distally; the cuneiform (as in Choloepus q.v. p.136) is almost part of the ulna. In Macropus rufus, flexion reaches 120°, and hyperextension is less than 10°, measuring in this case between the long axes of the ulna and metacarpal 3. The radius is strongly bowed, and difficult therefore to use for this measurement. On the radial side of the carpus, the scapholunar rocks on the flexor margin of the radius, parting widely from it the majorum of the radius, to give over 100° of flexion, and 20° of flexion on the scapholunar. At the ulnar side, the cumsiform slides flexad round the ulna to give 50° flexion, and the unciform slides extensad on the cuneiform, and parts from it extensed, a further 70°. Deviation, from 10° radial to 20° ulnar is produced entirely at this "proximal" joint, by the scapholunar sliding ulnad or radiad across the radius and unciform similarly across the cuneiform.

The smaller macropid shows an interesting difference from M. rufus in that some 50° hyperextension is obtainable at the wrist. This is not due, however, to a different form of the proximal joint, and the proximal carpal bones move the same amount on the forearm skeleton. However, the radius is

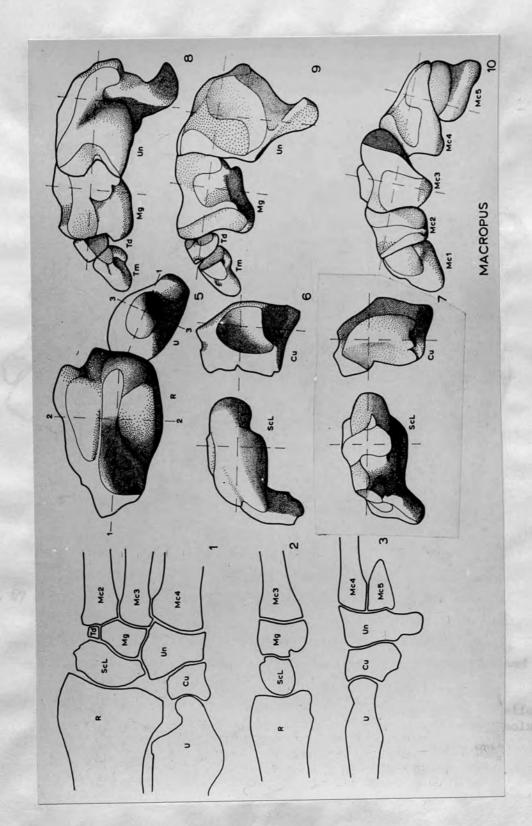


Fig. 66 Carpal diagram of Macropus.

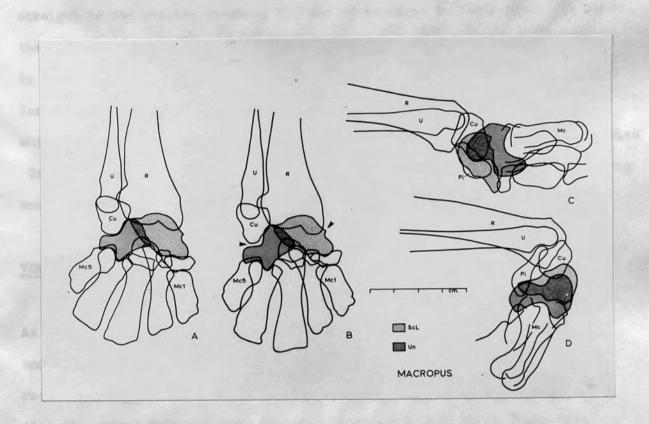


Fig. 67 Action of the carpus of Macropus, drawn from radiographs.

- A Extensor view, ulnar deviation.
- B Extensor view, radial deviation. Most of the movement is due to the scapholunar and unciform sliding past radius and cuneiform.
- C Radial view, extension.
- D Radial view, flexion. There is some movement of the cuneiform on the ulna, but most of the flexion is between the scapholunar and the radius or the unciform and the cuneiform.

straight in the smaller species, instead of bowed as in the larger. It seems that this bowing results in the metacarpals being in line with the forearm in hyperextension, and better able to support weight. During grazing, the larger macropids frequently support themselves on their forelimbs and tail while moving the hindlimbs forward. It seems probable that the smaller species do not do this (in the specimen examined, the claws of the forelimb were long and unworn) or if they do, are not heavy enough to need this adaptation.

VOMBATUS

As seen in RUS, however, the scapholunar is less curved, and the unciform and magnum together form a convex surface at the mid-carpal joint, faintly resembling that of primates. Hyperextension is limited to about 50°, so that the animal does not have strictly plantigrade forelimbs. There are, however, large plantar pads which help give support to the foot and the form might be regarded as semi-digitgrade (this is comparable with the status of the elephant as unguligrade). Hyperextension at the metacarpophalangeal joints, as in, for example, carnivores, is of considerable importance, reaching 70°. Flexion reaches 90°, and as in Macropus, most of the movement due to the scapholunar and unciform flexing on the radius and cuneiform respectively, as the cuneiform only flexes 20° on the ulna. (fig. 69, p. 189).

Deviation resembles that in the primates, but in reverse. Ulnar deviation, to 20°, is produced at the mid-carpal joint by the magnum and unciform sliding radiad on the cuneiform and scapholunar - the trapezoid gets parted from the

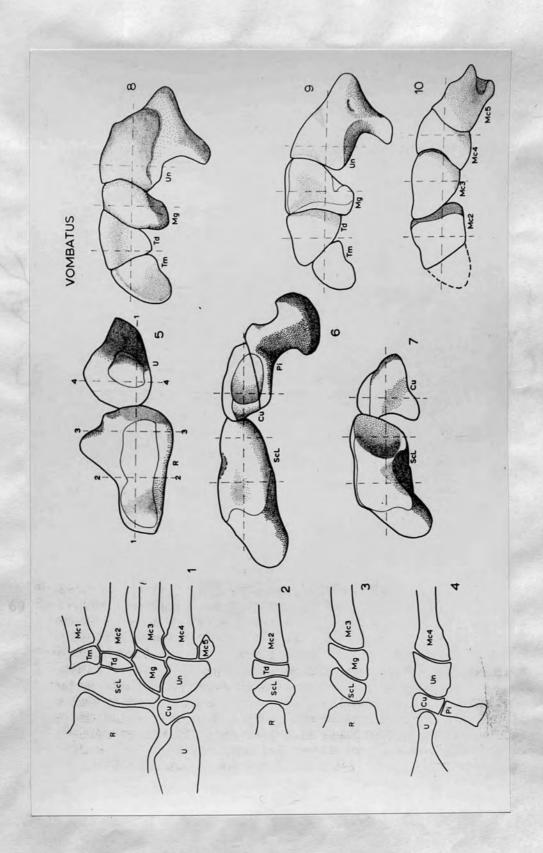


Fig. 68 Carpal diagram of Vombatus.

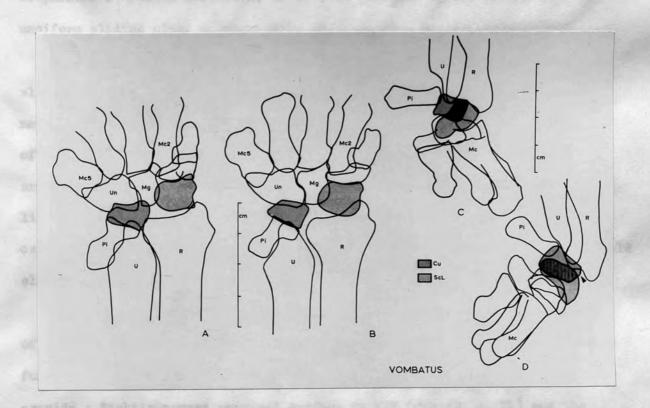


Fig. 69 Action of the carpus of Vombatus, drawn from radiographs.

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- A Extensor view, ulnar deviation.
- B Extensor view, radial deviation. The amount of movement shown is much less than can occur. The magnum and unciform have slid round through 100 past the scapholunar and cuneiform.
- C Radial view, hyperextension.
- D Radial view, flexion. There is some flexion of the cuneiform on the ulna. The most significant movement is between the scapholunar and the radius. As in carnivores, the scapholunar rocks on the flexor lip of the radius in flexion, and they are widely parted on the extensor side.

scapholunar. Radial deviation, to 10°, is produced by the scapholunar and unciform sliding ulnad on the radius and cuneiform respectively.

Diprotodon is interesting as a form closely related to Vombatus and always restored with completely plantigrade forelimbs, that is with the metacarpals and all parts distal lying flat on the ground. Examination of the specimen in the British Museum shows that the carpal bones are artificially parted to achieve this. It seems very probable that Diprotodon, like Vombatus was semi-digitgrade, and had a fibrous pad supporting the carpus (fig. 70, p. 191). As in Vombatus, the metacarpo-phalangeal joints would allow considerable hyperextension.

<u>Phascolarctos</u> is another form closely resembling <u>Vombatus</u> in the form of the carpus, but as might be expected in an arboreal form, the deviational function of the wrist is emphasised. The unciform and scapholunar, together provide a <u>tightly curved</u> proximal surface in RUS (fig. 62, p. 173) and the possible range of movement is 30° ulnar to 30° radial deviation.

THYLACINUS

This animal is interesting since, although it shows a striking, convergent, resemblance to a canid, the carpus remains very dissimilar. In a canid, the scaphoid and lunar are fused, provide a deviational as well as a flexion hinge, and there is a prominent tubercle on the flexor side with which the scapholunar rocks over the flexor edge of the radius. In <u>Thylacinus</u> the scaphoid and lunar are separate, do not show a smooth, convex proximal surface in RUS (fig. 71, p. 193), and there is no tubercle on the scaphoid. In FES, the proximal surface of the scaphoid changes from concave extensed to convex flexad. The

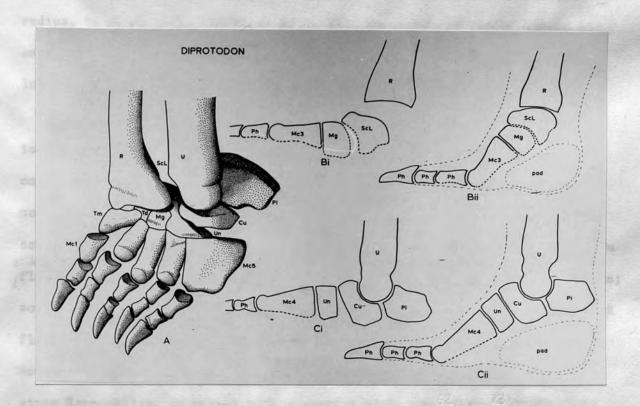


Fig. 70 Carpus of Diprotodon.

- A Drawing of the manus of the mounted skeleton.
- B FES through the radial side of the carpus.
- C FES through the ulnar side of the carpus.

Bi and Ci show the specimen as it appears to be mounted. Bii and Cii suggest what is felt to be a more likely pose. Probably, as in Proboscidea and in <u>Vombatus</u>, there was a large fibrous pad supporting the carpus.

lunar is very small and rounded in section. The distal surface of the radius, to which these two bones articulate, is generally rather convex in section, but with a groove running obliquely down the ulnar side for the lunar and a distinct notch in the flexor border.

Flexion at the proximal joint, from a position of 30° hyperextension to at least 70° of flexion involves the scaphoid and lunar sliding flexad on the radius, and the flexo-ulnad corner of the scaphoid slides into the notch on the flexor border of the radius while the more radial side of the scaphoid slides round the "higher" radial edge of the radius. The cuneiform slides flexad round the ulna, though not so far as the scaphoid moves on the radius; some flexion occurs between the cuneiform and unciform. It is probable that flexion in life would go much further than just 70°; requiring further movement of the scaphoid on the radius, and the unciform on the cuneiform, since Sarcophilus, an animal with a shorter hand, can obtain 160° flexion; this is difficult to judge from skeletal material, since it requires extreme parting at the extensor side of the carpus. It is perhaps worth mentioning that flexion in Thylacinus and the other marsupials causes some ulnar deviation (15° in this case) just as in carnivores, and for the same mechanical reasons.

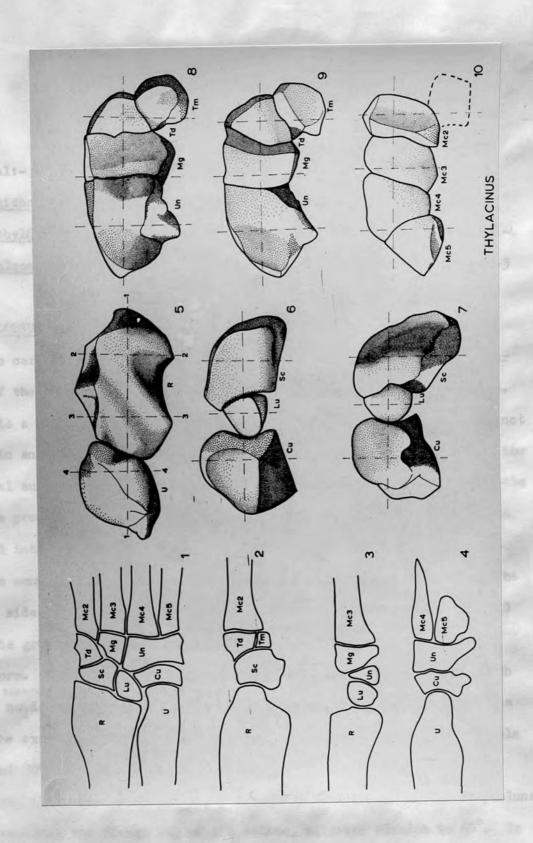


Fig. 71 Carpal diagram of Thylacinus.

MON OTREMATA

Material:-

Ornithorhynchus anatinus - platypus - skeletal BM(N.H.) 735g

Tachylcossus aculeata - echidna - skeletal BM(N.H.) 1955-11-24-4

Zaglossus sp. - echidna - skeletal BM(N.H.) 1959-5-25-3

TACHYGLOSSUS and ZAGLOSSUS

The carpus of the echidnas may be considered first, since the larger size of the bones makes a full description easier than for the platypus. There is a scapholunar bone which Holmgren (1952) shows to be two distinct bones in an embryo, but there is no trace of a centrale. The shape of the proximal surface of the scapholunar differs radically from that of all the mammals previously considered. It is convex in FES (fig. 72, p. 195), and divided into two condyles by a groove. The distal surface of the radius has two concave facets separated by a ridge to articulate with this. The distal side of the ulna is the converse of this, a convex surface in FES which is grooved to take a concave (in FES) but wedge shaped (in RUS) cuneiform. The overall effect is a double flexion-extension hinge which allows no deviation. The trochleated surface of the scapholunar extends onto the extensor surface of the bone, so that hyperextension is possible to about 70°; the monotremes have truly plantigrade fore feet. In the echidnas, there is a deep concavity below the flexor edge of the scapholunar, which receives the flexor lip of the radius, allowing flexion to 60°. In hyperextension, while the radius slides extensad on the scapholunar, the ulna

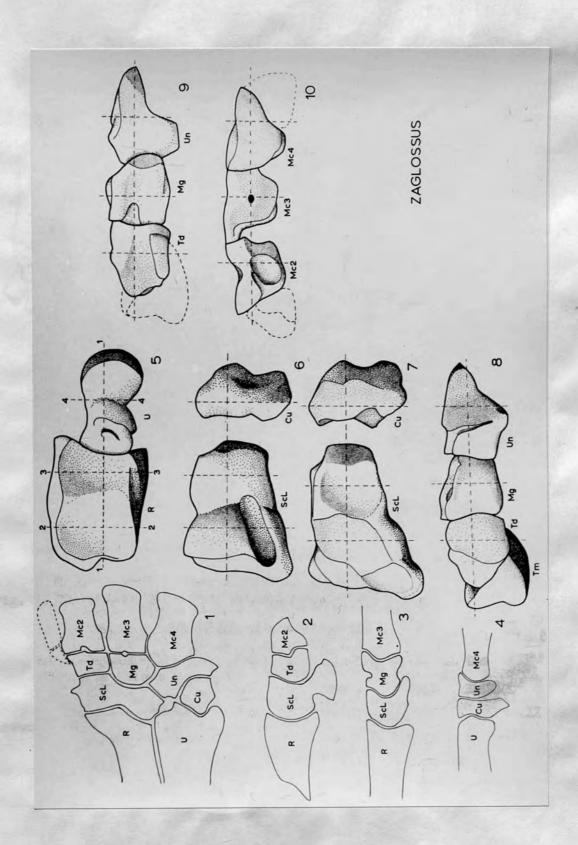


Fig. 72 Carpal diagram of Zaglossus.

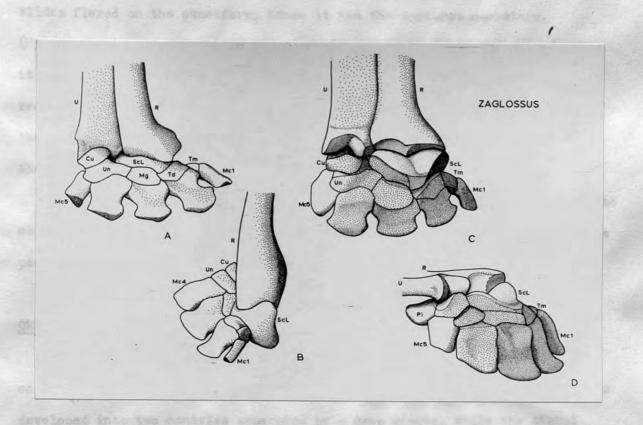


Fig. 73 Action of the carpus of Zaglossus.

A Hyperextension, seen in extensor view.

author of the radius has a projecting tenger or the line touch

- B Hyperextension, seen from radially.
- C Flexion, seen in extensor view.
- D Flexion, seen in oblique ulnar-distal view.

The pulley-like nature of the proximal joint, where all the movement occurs, is evident.

slides flexad on the cuneiform, since it has the converse curvature. (Hyperextension at the carpus occurs while the manus is on the ground, so it is reasonable to talk of the forearm bones moving on the carpals). This results in some 30° of radial deviation accompanying hyperextension so that the elbow must move outwards from the body (abduct) during retraction of the forelimb.

The mid-carpal joint is very irregular in RUS, and it seems to contribute nothing to the activity of the wrist, though some flexion would appear to be possible to judge from the appearance of the bones in FES.

ORNITHORHYNCHUS

The functional plan of the carpus in the platypus is the same as in the echidnas, but even more extreme. The proximal surface of the scapholunar is developed into two condyles separated by a deep groove, while the distal surface of the radius has a projecting tongue on the flexor border fitting below this groove. The extensor surface of the scapholunar has a depression which receives the extensor margin of the radius, allowing a full 90° hyperextension. There is probably no functional significance in this extra 20° of hyperextension, as the greater thickness of the carpus of Tachyglossus results in the hand being flat on the ground and the forearm vertical with only 70° hyperextension. Peculiarly, the projecting lip of the radius seems to prevent the proximal joint being flexed beyond the straight, extended position, and only 20° of flexion seems possible, most of this being due to the carpo-metacarpal joint.

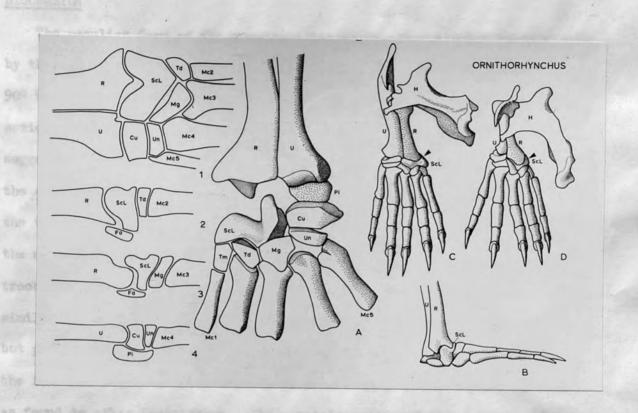


Fig. 74 Carpus of Ornithorhynchus.

1-4, diagrammatic sections of the carpus.

A Extensor surface of a partly "exploded" carpus.

B Manus drawn in radial view, to show full plantigradism, with considerable hyperextension at the proximal joint.

C, D Forelimb skeleton from above; C in protraction, D in retraction.

(Fa, falciform, or radial sesamoid; H, humerus)

DISCUSSION

The peculiar form of the monotreme carpus is matched among mammals only by that of the talpid moles. Both groups have the ability to produce about 90° hyperextension at the proximal carpal joint, and have a similar duplex articulation between the radius and the carpus. In the introduction, it was suggested that the mammalian tarsus had evolved a hyperextending joint in the shape of the astragalo-tibial joint (p. 18) and that this was contrary to the trend in the carpus. It is evident that the moles and, more especially, the monotremes have in the proximal carpal joint something resembling the trochleal joint of the mammalian ankle. Reed (1951) comments on the general similarity of the forelimbs of Neurotrichus (a talpid) and Ornithorhynchus, but points out that this must be an example of convergent evolution, since the forelimb of the talpids must be derived from a normal therial forelimb as found in other Insectivora. The possible origin of the monotreme forelimb requires further consideration.

So far as the manus is concerned, in addition to the peculiar nature of the carpal joints, the monotreme hand is unusual in that the metacarpophalangeal joints are not flexion-extension hinges. In therian mammals, these joints are the main hyperextension hinge which allow the vertical part of the limb to move on the grounded part of the foot, and with the interphalangeal joints also allow flexion movements which fold the hand. Even the manus of the talpids retains some flexion-hyperextension capability at these joints, though since the hand of the more extremely modified talpids cannot be placed flat on the ground, this capability could be expected to have been lost. In the monotremes, there is no trace of the metacarpo-phalangeal joints being,

or having been, flexion-extension joints. Only at the distal interphalangeal joint is movement in this plane possible, from 60° hyperextension to 50° flexion. Had such movement been possible at the other phalangeal joints, it is very unlikely on functional grounds to have been lost. The conclusion is that the monotreme limbs have never been in a stage resembling a primitive therian. It is generally agreed that the monotremes have had a separate origin among the most mammal-like reptiles from the therian mammals (Kühne 1956; Kermack and Mussett 1958; Simpson 1961 etc.); their limb structure strongly supports this conclusion, as Kühne concludes. Parrington (1961) in an authoritative account of the femur in mammal-like reptiles suggests that the monotreme pelvic girdle and musculature are so mammalian in form that the sprawled limb position, with the femur and humerus held horizontally, must be secondary. My own feeling is that the principal action in the locomotion of these forms is not retraction of the limb, as is the case in lizards, where the humerus and femur are pulled back in the horizontal plane, or as in therian manmals, where the limb is pulled back in the verical plane. It seems likely that in monotremes the humerus and femur are axially rotated, as is the humerus of the mole. The peculiarly mammalian form of the pelvic architecture in the monotremes would be as well adapted to produce this movement of the femur as it would to produce the usual mammalian movement. In this case the resemblance of therian and monotreme pelvis is an extreme case of convergence. As other evidence for the view that monotreme limbs have never attained the therian limb position, the following may be mentioned; 1) The radius lies wholly medial of the ulna. In all other mammals, the

radius is anterior to the ulna at the proximal end, and crosses in front

of the ulna to reach the medial border of the hand. Even Oligokyphus,

which Kühne shows to resemble the monotremes very closely, has the radius anterior to the ulna at the proximal end. In the talpids, the forearm bones remain parallel for the full length of the forearm, but this is because the distal end of the radius, as well as the proximal end, is morphologically anterior to the ulna.

- 2) Perhaps correlated with the previous point, the ulna and radius articulate by a continuous concave facet to a single condyle on the humerus, (Simpson 1928). Usually in therians, the ulna articulates to a groove alongside a condyle for the radius.
- 3) The peculiar form of the tarsus also suggests that the therian limb position has never been obtained. The calcaneum is small, has a small tuber directed laterally ("fibulad") to the foot (though posteriorly to the animal, as the foot itself points laterally) and, so far from underlying the astragalus, has an articular surface for the fibula (fig.75, p.202). The fibula articulates to the astragalus as well as the calcaneum, the articulation being more proximally placed than that for the tibia, which extends down the medial (anterior) side of the astragalus and articulates there into a concavity. (In placentals, the fibula extends further distally than the tibia, while in marsupials the articulation is similar to placentals or the two bones articulate on the same level.) Gregory (1910) mentioned some of the peculiarities of the tarsus in monotremes.

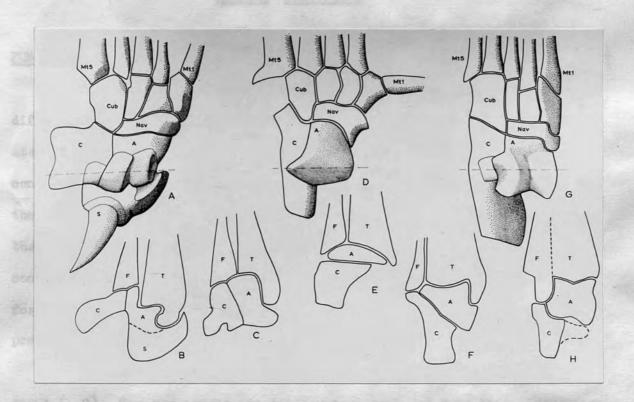


Fig. 75 Comparison of the tarsus of monotremes and therians.

- A Ornithorhynchus. Dorsal surface of tarsus.
- B Ornithorhynchus. Section through tarsus along the plane indicated in A.
- C Tachyglossus. Section through tarsus in similar plane to B.
- D Phalanger. Dorsal surface of tarsus.
- E Phalanger. Section through tarsus.
- F Macropus. Section through tarsus.
- G Erinaceus. Dorsal surface of tarsus.
- H Erinaceus. Section through tarsus.

Abbreviations - A, astragalus; C, calcaneum; Cub, cuboid; F, fibula; Mtl, first metatarsal; Mt5, fifth metatarsal; Nav, navicular; S, spur; T, tibia.

GENERAL DISCUSSION

FUNCTIONAL TRENDS

The main part of this work has necessarily been a catalogue of the different types of mammalian carpus and their function, and as such must stand largely without further comment. However, a few general inferences connecting the "primitive mammalian carpus" of the introduction (p.8) with the different types of carpus are obviously desirable. It is unfortunate that these can only be inferences, but better established phylogenetic connections would require a more thorough knowledge of the carpi of various fossil forms, particularly Palaeocene and Eocene mammals, which is not at present available.

The primitive therian carpus was presumably arranged as indicated in fig.1 (p.9). (The monotremes are deliberately excluded from this discussion since, as has just been suggested, they probably never attained a limb structure or gait resembling that of the therians). The ulna ended in this primitive condition as a convex, condyloid, styloid process, articulating with a shallow concavity formed by the proximal surface of the cuneiform. The distal surface of the radius and the distal surfaces of the proximal row of bones were presumably concave, opposing convex proximal surfaces of, respectively, the proximal or distal rows of carpal bones. This duplex form of proximal joint (concavo-convex radially, convexo-concave on the ulnar side) was presumably a result of the primitive limb position of ancestral mammal-like reptiles. With the sprawled limb position and the humerus held more or less horizontally, the main for the limb action in

locomothion would retraction of the humans from an antero-laterally pointing position to a postero-laterally directed position. This would require some rotation between the bones of the forearm and the hand on the ground as the body moved over it (fig. 76, p. 205). This rotation could readily be provided by the styloid process of the ulna pivoting on the cuneiform. The radius would ride over the extensor surface of the opposing carpal bones.

This primitive therian carpus must have been capable of producing both flexion and deviation at both the proximal and mid-carpal joints. The development of the ability to produce flexion can be traced through a morphological series which may well indicate a phylogenetic trend (fig. 77, p. 206). In the simplest condition, the form of both joints (proximal and mid-carpal) is a shallow concavity, in FES, with convex surfaces articulating into it. In flexion, the convex proximal surfaces of the carpal bones cause them to slide extensed (fig. 3%, p. 26). This joint form is probably not very stable as a weight bearing surface, but allows a moderate amount of flexion and a moderate amount of hyperextension. As such it is found in many primates, including Homo, in sloths and in Tamandua. The amount of movement of one bone past another like this is probably limited, by the need to retain some joint stability and prevent dislocation, to the exposure of about half the bone surface, perhaps 500 of flexion (or hyperextension). The same joint form can provide rather more flexion, for allowing the hand to clear the ground during limb protraction, if the potential to produce hyperextension is sacrificed, and added instead to the amount of flexion possible. The straight, extended, position of the wrist is then the most extended position

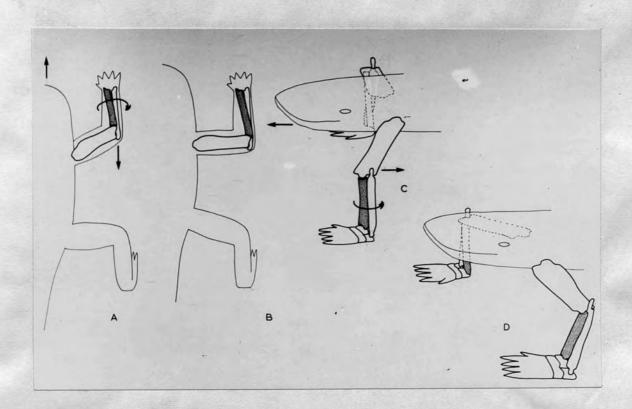


Fig. 76 Twisting action of primitive tetrapod forelimb. Not only do the radius and ulna twist round one another, but they must also spin on the hand which is flat on the ground.

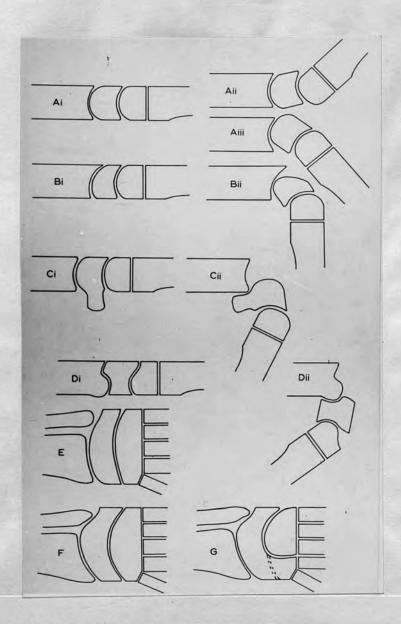


Fig. 77 Suggested morphological series of carpal hinges.

A-D as a flexion hinge.

A The proximal bone at each joint is gently concave. Moderate hyperextension (Aii) and flexion (Aiii) are possible, (e.g. most primates, sloths).

B As in A, but with some alteration of aspect of the joint surfaces, so that there is no hyperextension, all the possible movement being used in flexion (Bii), (e.g. Myrmecophaga, Mandrillus).

C The scaphoid develops a "heel", enabling it to rock on the flexor lip of the radius (Cii) giving more flexion than is possible in B, (e.g. carnivores).

D The flexor lip of the radius as in C is enlarged into a convex surface, round which the proximal carpal rides. This is a firmer joint than C, and the mid-carpal joint is better developed as a flexion hinge, (e.g. most ungulates).

E-G as a deviation hinge.

E Both proximal and mid-carpal joints are gently curved (e.g. Rattus).

F Both curves are steeper.

G The chord of one curve or the other is shortened, by the exclusion of one (or more) bones. In primates, as here, the mid-carpal joint is shortened, in Choloepus, the proximal joint is shortened.

attainable, and more stable for weight bearing. This is the condition found in Myrmecophaga and the ground sloths, where the amount of flexion possible is around 90°.

Further flexion than this, necessary particularly in those quadrupedal forms which have a rather long manus, requires a further development of the flexion hinge. This takes the form of a tubercle on the scaphoid, or scapholumar, which projects on the flexor surface of the carpus. In flexion, the convex body of the scaphoid slides extensad on the radius (that is the "primitive" movement just described) until the base of the tubercle meets the flexor lip of the distal surface of the radius. The scaphoid then rocks on the flexor margin of the radius, pivoting on the base of the tubercle, so that the body of the scaphoid parts from the radius. This is the condition found in the carnivores, and in some rodents (e.g. Cavia, Castor) and insectivores (e.g. Sorex, Erinaceus). It may allow as much as 120° of flexion at the proximal joint, in addition to the amount of flexion possible at the mid-carpal joint.

The condition of the carpal joints in the ungulate groups represents a logical extension of this. The flexor margin of the radius is thickened into a curved, convex (in FES) surface, and the base of the tubercle is equally developed into a concave surface which in flexion slides round it. This would seem to be a rather more dynamically stable action than the rocking of the scaphoid (or scapholunar) required in the carnivore type just discussed. Moreover, in equids and ruminants, the old, convex, more extensor placed surface on what was the body of the scaphoid is developed into a stop facet, providing a very stable joint form in the extended, weight bearing

static position of the limb. Stop facets are also developed in the mid-carpal joint in these forms, though as a flexion hinge it retains its primitive action. That is, the proximal surfaces of the unciform, magnum, etc., are convex, and slide extensed in flexion on the concave distal surfaces of the proximal bones. (fig. 77, p. 206).

The development of the carpal joint as a flexion hinge, can thus be related to the cursorial ability of the mammal concerned, at least in a general way. The development of the carpal joint as a deviational hinge can be similarly related to the arboreal ability; while the reduction in the deviational ability is probably also related to the cursorial ability. Presumably in the primitive condition both proximal and mid-carpal joint had a gently concave form proximally with concave surfaces articulating with them (as seen in RUS) and were capable of producing some deviation. The articulation between the ulna and cuneiform was, of course, of the opposite form, but presumably this joint was a sufficiently loose fit not to interfere with deviational movements resulting from the scaphoid and lunar sliding on the radius. This simple condition would allow perhaps 300 - 400 of deviation (this is the amount of deviation produced at the carpi of mammals which are not especially arboreal, such as some rodents and carnivores). Simply increasing the curvature of the joint surfaces in this plane, as in the sloths, can increase the amount of deviation which may be produced at the wrist to 80°. As a special case of this, the functional curvature of a joint can be increased by excluding some of the bones from the functional joint. This shortens the chord of the curve to the width of the bones remaining in the functional joint. As has been mentioned, this occurs in

the mid-carpal joint of some marsupials, and in primates where the magnum and unciform form the mid-carpal hinge in deviation, to the exclusion of the trapezium and trapezoid.

The reduction of the deviational ability of the carpus may affect just the mid-carpal joint, as in carnivores and most insectivores where this joint is solely a flexion hinge. Alternatively, as in the ungulates, both mid-carpal and proximal joints are solely flexion hinges. However, the need, already considered in the introductory section, for ulnar deviation accompanying flexion to swing the legs past one another complicates the hinge. Where the proximal joint retains some deviational ability, this can be used in comfunction with flexion to provide this lateral swinging. In the ungulates, some special provision for this is necessary, and generally the bones on the radial side of the carpus flex round a larger surface than those on the ulnar side. The subungulates (Hyracoidea, Proboscidea) retain some deviational ability at the mid-carpal hinge, and presumably use this to supplement the ulnar deviation from the proximal joint which accompanies flexion.

THE FUSION OF CARPAL BONES

Bearing in mind the trends just outlined, some suggestions can be made regarding the patterns of bone fusion seen in the carpi of different animals. The most common case is the fusion of the scaphoid and lunar in carnivores, and many rodents, insectivores and marsupials. The retention in these forms of the proximal joint as a deviational hinge means that the scaphoid and lunar together must provide a smooth convex surface to slide on the radius. This in itself might lead to, or be aided by, fusion of these two bones,

together with the fact that their distal surface provides the bearing surface for a flexion hinge, at the mid-carpal joint. This is particularly important when it is remembered that the flexion hinge at the proximal joint in these animals involves the scapholunar rocking on the flexor lip of the radius, so that the main body of the bone is widely parted from the radius. Any parting of the scaphoid and lunar which might result from this if the two bones were not fused would affect the form of the mid-carpal joint.

Another frequent occurrence is the disappearance of the centrale as a separate bone. In many cases (e.g. Erinaceus, Hystrix) the fate of the bone is just not known. In the carnivores and at least some insectivores (Sorex), however, it is known to be fused to the scapholunar. The reasons for this depend on the functions of the mid-carpal joint. Where this retains some deviational ability, the centrale moves with the bones of the distal row across the scaphoid and lunar. In flexion, however, it tends to remain with the proximal bones, the scaphoid and lunar, while the distal bones flex past it. Thus in forms like Castor and Rattus, where the mid-carpal joint is both a flexion and a deviation hinge, the separate centrale is present. In the carnivores, however, the mid-carpal joint is just a flexion hinge, and the centrale is fused to the scapholunar, providing a keel past which the magnum and trapezoid flex. In the hyracoids, the mid-carpal joint appears to be solely a deviational hinge, and the centrale is often fused to the trapezoid, on the distal side of that joint. In Talpa, although the midcarpal joint is not a deviational hinge, spreading of the hand occurs from there, and is a similar movement; the centrale here is a separate bone, and moves also on the scaphoid in flexion. The fusion of the centrale to the

scaphoid in <u>Homo</u>, <u>Gorilla</u> and <u>Pan</u> has already been mentioned, and it is suggested that this is at least consequent upon the reduction in the amount of deviation which can be produced at the mid-carpal joint; a separate centrale is able to move across the scaphoid under "lateral" pressure from the bones of the distal row.

Other cases of fusion between carpal bones are mostly rather unimportant from a functional point of view. In Equus and the ruminants the bones of the distal carpal row tend to fuse, but this is consequent upon the fusion of the metacarpal bones. This in itself is rather outside the scope of this account, but Smith and Savage (1956) have already suggested that fusion of the metacarpals results in a lighter structure with the same strength as separate bones.

TUBERCLES

This study of the wrist has concentrated on explaining the possible movements of the joint in terms of the shapes of the articular surfaces of the bones involved. However, Hughes (1944), considering the primate carpus, drew attention to the carpal tunnel as a feature of possible importance. The tendons of the flexor muscles cross the carpus in a groove which is roofed by the annular ligaments. The sides of the resultant tunnel may be reinforced by flexor hooks or tubercles on the carpal bones. Hughes shows that in Erinaceus the tubercle of the scaphoid on the radial side and the pisiform on the ulnar side contribute to the walls of the carpal tunnel, and takes this, reasonably, to be the primitive condition. In Homo, by contrast, this bony support is sited further distally, provided by the hook

of the unciform on the ulnar side and by the trapezium radially. Hughes suggests that this distal position of the bony supports is correlated with the lateral distortion of the flexor tendons in deviation, and suggests that the supports prevent interference with the tendons. It is perhaps unfortunate that Hughes did not examine any mammals other than primates in which the deviational ability is well developed, for the carpus of the sloths is particularly interesting on this point. As a sloth climbs along below a branch, each hand is placed ahead of the body with the wrist in sharp ulnar deviation, and the body is pulled up to the hand by the action, largely, of the flexor and extensor carpi radialis muscles. The range of deviation (abduction and adduction on Hughes' terminology) is greater than in Homo (70° or 80° against 55°) as shown not only by my own osteological studies but also by the photographs in Muybridge (1957). On Hughes' hypothesis, the bony supports in the ulnar side of a carpal tunnel should be well developed, but only the radial side has such processes. Both the scaphoid and the trapezium/metacarpal 2 (the latter are fused) have strong flexor hooks. As pointed out (p. 138) the sloths are unusual in that the flexor carpi radialis inserts onto the scaphoid (Choleopus) or trapezium (Bradypus), onto these hooks in fact. Indeed, the origin or insertion of a muscle (or possibly a ligament) seems a much more likely reason for the presence of prominences on the flexor side of the carpus, in this case and in others. In Homo, the hook of the unciform receives the flexor carpi ulnaris tendon via the pisiform, while the trapezium is the point of origin of several of the short muscles to the thumb (particularly the opponens pollicis and part of the flexor pollicis brevis). Attention has also been drawn (p.105) to the flexor hooks

developed in some ungulates (Rhinocerotidae, Tapiridae, Suina etc.) on the magnum and unciform which appear to take the ligaments that cover the flexor side of the carpus. It is worth noticing that these hooks are well developed in the ungulates which have not developed stop facets, but not present in those (Equidae, Tylopoda, Ruminantia) that have.

FURTHER PROBLEMS

It seems appropriate to end on some suggestions for further work which is needed on this subject, and further work which might develop from it.

- A. Consolidation. Attention has already been drawn to the fact that the examination of fresh dead material has been by far the most satisfactory. Several animals have been mentioned which have so far been studied from skeletal material only and would benefit from the examination of fresh dead material. Orycteropus is the prime example of this, but others include Prioden, Procavia and Ateles or Hylobates.
- B. Phylogenetic Considerations. There is perhaps only one group where the present studies, of themselves, suggest further work from this point of view. This is the pinnipedes. It is usually said that the Otariidae, having the ability to use both fore and hind limbs on land, are more primitive (in this respect) than the Phocidae. The examination of the carpus has suggested that this might be illusory, for the phocid carpus is more like a fissipede's in form than is that of an otariid, while the nature of the hyperextension hinge which the latter use to get the foreflipper flat on the ground is quite unique. Examination of the tarsus might be rewarding.

C. The biggest gap in this work, as already hinted at the beginning of the general discussion, is the lack of evidence on the carpal function of the fossil forms. There are three areas in which this ought to be improved. Firstly, a number of orders of mammals, particularly early ungulates and the "South American ungulates", have not been examined at all. Secondly, several groups which might help to establish, or contradict, the suggested phylogenetic trends, might be examined. For example, the artiodactyls are considered to be very closely related to the carnivores by way of certain creodont genera. Yet my suggestions on functional trends in the development of the carpus as a flexion hinge suggest that the perissodactyl carpus is rather nearer to the carnivore type. Certainly the carpus of some of the earlier creodonts might prove interesting. Thirdly, there is the possible importance of even earlier forms, the mammal-like reptiles, to consider. These might be important for indicating whether the "primitive mammalian carpus" of the introduction and elsewhere in this account really existed, and might also indicate whether the monotremes are as isolated in limb form as I have suggested. Even if a full functional interpretation of the fossil forms is not possible, a description of the carpal bones in the manner used here, and particularly the diagrammatic sections, would be more useful for considering the bones in functional terms than the, too frequent, listing of the bones present.

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The genera are arranged in the order used by Simpsob, G.G., 1945 (hall

APPENDIX

Table of Movements.

The following table for the angular movements occurring at the carpus is presented as a summary of the various figures which have been quoted in the text. It has already been emphasised that these measurements are not, and cannot be, particularly accurate; apart from the innaccuracies of measurement and the inadequacy of some of the material, different individuals of a species, or one individual on different occasions, may give very different values. The figures do show, however, the relative importance of deviation in arboreal forms, and the range of flexion ability in different animals.

The importance of the different methods of study used in regard to the reliability of the results obtained has already been stressed (p. 35). In the table, these are abbreviated as follows:-

- c casting, i.e. Johnston's method
- f manipulation of fresh-dead material
- p embedded pins
- pr manipulation of preserved material
- s manipulation of skeletal material
- ss serial sections
- xf x-radiographs of fresh-dead material
- xs x-radiographs of skeletal material

The genera are arranged in the order used by Simpson, G.G., 1945 (Bull. Amer. Mus. Nat. Hist. 85)

- ? indicates information not available, <u>usually</u> through unsuitability of method.
- indicates no apparent movement.
- # fossil groups.
- (1) figures given by Wright, R.D., 1935, J. Anat. 70
- (2) figures obtained from the x-radiographs in Johnston T.B. et al. 1958, Gray's Anatomy 32nd Edition.

Animal Method		Flexion			Hyperextension			ation	Totals	
			Total			Total	Ulnar	Radial	Flexion Extension	Deviat
κχ	60	-	60	70	_	70	-	-	130	-
s f s s xf p f	25 130 70 60 70 105 110	25 30 ? 20 10 19 5	50 160 ?70 90 90 121 120 120	55 40 30 ? 50 6	? ?	55 40 ?30 ? 50 6 -	40 10 ? 30 20 20 ? 20	10 20 ? 30 10 - ?	105 200 100 ? 140 127 120 130	50 30 ? 60 30 20 ?
f ss ss	50 40	60 70 -	120 130 30	50 65 70	20	50 65 90	20 10 -	15 30 -	170 195 120	35 40 -
s	60	30	90	20	-	20	30	10	110	40
s	20	80	var.	-	-	-	-	-	100+	-
	? -30 65 40 60 10 50 30	? 70 40 73 60 70 40 70 40 50	70 70 80 150 96 135 60 120 70 80	? 40 30 10 20 25 20 15 20 28	? 5 - 10 - 16	40 45 35 10 20 25 30 15 20 44	30 35 20 ? 45 30 30 30 ?	40 30 5 ? 15 15 20 ? 22	110 135 130 160 116 155 90 135 90	50 70 65 25 60 45 50 54 58
	sf s s xf pf f ssss s s s s s s pf f s s	Prox joint \$\frac{1}{50} \text{ for } 60 \\ \$\frac{1}{50} \text{ s } 60 \\ \$\frac{1}{50} \text{ s } 60 \\ \$\frac{1}{50} \text{ for } 110 \\ \$\frac{1}{50} \text{ s } 60 \\ \$\frac{1}{50}	Prox Mid-c joint joint \$\frac{1}{5}\text{ 60} -	Prox Mid-c Total joint joint joint joint \$\frac{1}{2} \text{ for a constant joint} for a const	Prox Mid-c Total Prox joint joint joint joint joint \$\frac{1}{2}\$ 25 25 50 55 \$\frac{1}{2}\$ 130 30 160 40 \$\frac{1}{2}\$ 70 ? ? ? 70 30 \$\frac{1}{2}\$ 8 60 20 90 ? \$\frac{1}{2}\$ 70 10 90 50 \$\frac{1}{2}\$ 105 19 121 6 \$\frac{1}{2}\$ 110 10 120 10 \$\frac{1}{2}\$ 50 60 120 50 \$\frac{1}{2}\$ 55 50 55 \$\frac{1}{2}\$ 60 20 90 ? \$\frac{1}{2}\$ 70 10 90 50 \$\frac{1}{2}\$ 105 19 121 6 \$\frac{1}{2}\$ 100 10 10 10 10 10 10 10 10 10 10 10 10	Prox Mid-c Total Prox Mid-c joint joint join	Prox Mid-c Total joint j	Prox Mid-c Total joint J	Prox Mid-c Total prox Mid-c Total Ulnar Radial joint joint joint Total Ulnar Radial joint joint Total Joint Ulnar Radial joint joint Total Ulnar Radial Joint	Prox Mid-c Total Prox Mid-c Total Ulnar Radial Flexion joint joint joint Total Ulnar Radial Flexion Extension S

Animal Method		Flexion			Hyperextension			Devia	tion	Totals	
		Prox joint	Mid-c joint	Total		Mid-c joint	Total	Ulnar	Radial	Flexion Extension	Deviat
Edentata											
Myrmecophaga		55	20	85	15	-	15	30	30	90	60
11	f	90	20	110	10	-	10	30	20	120	50
Tamandua	S	-	30	30	50	30	80	10	20	110	30
11	f	60	-	60	60	20	80	20	50	140	70
11	xf	40	20	60	40	40	80	30	40	140	70
Bradypus	S	20	20	40	40	-	40	30	30	80	60
Choloepus	S	30	40	30	55	-	55	40	30 30	85	70 85
Priodontes	xs s	35 10	50	75 60	50 40	-	50 40	55 15	-	125 100	15
Pholidota											
Manis	_	10	75	55	40	2/5	40	20	20	95	40
Manis	f	-	35 40	40	45	-	45	10	20	85	30
T o gomownho											
Lagomorpha											7.0
Lepus	xf	101	36	133	10	-	10	10		143	10
iii	f	90	55	145	-	-	-	10	-	145	10
Rodentia											
										7.00	
Sciurus	f	100	30	130	50	A THE	50	40	10	180	50
Castor	S	70	10	90	50		50	10	10	140	20 40
"	f	- 70	-	70	100	-	100	10	30	170 165	?
"	p	80	-	80	60	15	85	?	10	120	35
Pedetes	S	20	20	50 60	70 30		70 30	25 15		90	15
Hystrix	s f	50 80	30	110	30	-	30	10	-	140	10
Cavia		30	70	100	10		10	25	10	130	35
Hydrochoerus	S	50	70	100	10		10	-)	10	1,0	"
Carnivora (Fissipedia)											
Canis	s	90	40	130	40	-	40	15	15	160	30
Vulpes	c	110	40	154	-	-	-	?	3	154	?
Ursus	s	40	45	85	55	-	55	20	10	140	30
11	f	55	35	90	55	-	55	20	10	145	30
Galera	f	?	?	120	30	-	30	20	20	150	40
11	xf	73	34	110	50	-	50	?	?	160	?
Dicercia	p	95	30	135	40	30	70	?	?	200	?

Animal Metho	od	F	Lexion		Нуре	Hyperextension			ation	Tota	als
		Prox joint	Mid-c joint	Total		Mid-c joint	Total	Ulnar	Radial	Flexion Extension	Deviat.
Carnivora				,							
(Fissipedia)	Conti	nued									
Meles	f	80	40	120	10	-	10	15	5	130	20
-11	C	80	20	133	-	-	-	?	?	133	?
Enhydra	S	10	40	60	20	-	20	20	20	80	40
Viverra	S	40	20	80	50	-	50	15	15	130	30
Crocuta	S	90	30	145	45		45	10	5	190	15
Felis	f	120	40	170	40	-	40	10	10	210 205	20
Acinonyx	S	110	40	165	40	-	40	•	•	205	
(Pinnipedia)											
Zalophus	pr	20	-	20	-	70	90	30	30	110	60
Phoca	f	50	20	120	40	-	40	50	-	160	50
Pusa	f	50	20	120	20	-	20	50	-	140	50
Halichoerus	s	50	10	70	20	-	20	50	15	90	65
Ommatophoca	f	40	15	55	20	-	20	30	-	75	30
Tubalidentata											
Orycteropus	s	10	-	16	-	-	-	15	-	16	15
Proboscidea											
Loxodonta	s	90	-	90	-	-	•	10	10	90	20
#Embrithopoda											4
#Arsinoitherin	um s	80	-	80	-	-	-	10	10	80	20
Hyracoidea			,								
Dendrohyrax	s	70	20	90	20	-	20	20	10	110	30
Sirenia											
Trichechus	s	40	-	40		•	-	-	-	40	-
Perissodactyla											
Equus	p	90	50	150		-	_	-	-	150	-
II II	xf	79	52	140	-	-	-	-	- 5	140	-
Tapirus	S	70	40	110	-	-	_	-	-	110	-
Dicerorphinus		70	40	110	10	-	10	-	-	120	-
Ceratotherium		90	50	140	-	-	-	-	•	140	

Animal Method		Flexion			Hyperextension			Deviation		Totals	
		Prox joint	Mid-c joint	Total	Prox joint	Mid-c joint	Total	Ulnar	Radial	Flexion Extension	Deviat
rtiodactyla											
Sus	s	60	50	110	-	-	-	-	-	110	-
Hippopotamus	S	60	40	100	-	-	-	-	-	100	-
#Oreodon	S	50	40	90	-	-	-	-	-	90	-
	s	120	50	170	-	-	-	-	-	170	-
Llama		00	60	140	_	-	-	_	-	140	-
Llama Ovis	S	80	00	エー							
					-	-	-	-	-	150	-
Ovis	s p xf	75 93	65 73	150 163		-	-	-	-	150 163	-