209

lab study
animals caught 1981, 82

417

J. Zool., Lond. (*A*) (1986) **208**, 9–35

Morphofunctional study of the digging system of the Namib Desert Golden mole (*Eremitalpa granti namibensis*): cinefluorographical and anatomical analysis

J. P. GASC, F. K. JOUFFROY, S. RENOUS 1986
*CNRS Equipe "Locomotion animale", Unité 1137 associée au Muséum national d'Histoire naturelle.
Laboratoire d'Anatomie comparée, 55, rue Buffon, 75005 PARIS, France*

AND F. VON BLOTTNITZ
Postfach 971, 9000 Swakopmund, Namibie

(*Accepted 12 March 1985*)

(With 1 plate and 12 figures in the text)

Digging locomotion of Namib Golden moles has been studied by making X-ray cinematograph films, and the morphology of their locomotor system investigated by means of radiographs and dissections. Biomechanical interpretations of the data so obtained show that moving forwards results from a cyclical compacting and decompacting of the surrounding sand. The whole step-cycle is made up of a buttressing phase followed by several digging propulsion phases.

Contents

Introduction

Eremitalpa granti namibensis Bauer & Niethammer, 1959 is a subspecies of Golden mole which lives in the soft, shifting sand of the western Cape Coast and of the Namib Desert of South Africa. Within the family Chrysochloridae, *Eremitalpa* comprises with *Chrysospalax* the subfamily Eremitalpinae (Simonetta, 1957*a*) characterized by common dental features (Meester, 1964) and by the large size and spherical shape of the caput mallei, which is not enclosed in any tympanic bulla. These features, which make the malleus easy to spot in X-ray pictures, have been used as landmark in this study. Petter (1981) discussed the characters used in chrysochlorid systematics.

According to Holm (1969), the Namib Golden mole usually buries itself by noon down to 50 cm (depending on the external heat) to find a suitable temperature (25/26 °C). Emergence is reported to occur after dusk for nocturnal feeding activity. Holm's description of the locomotion in the field is mainly when the animal was totally emerged. Our own observations on captive animals agree with Meester's, who mentions animals remaining below the surface of the loose sand, down to 10 cm when resting, or burrowing just below the surface when active. A raised ridge at the surface

0022–5460/86/001009 + 27 $03·00/0

of the dune enables the observer to follow the underground travel of the mole. Such an observation has been confirmed by Coineau (pers. comm.). According to Shortridge (1942) and Roberts (1951), the animal moves in permanent tunnels when it is in a more solid sand (river sand).

Eremitalpa granti namibensis differs from other subspecies of *E. granti* in its capability of burrowing in a loose sand which crumbles as fast as it is penetrated by the head of the animal. In such sand, building tunnels is impossible; any space produced by the foreward movements of the animal is immediately filled by the falling sand. This Golden mole can breathe, move, rest and feed while buried: Holm (1969) found an average of 10 % of sand in stomach contents. According to Shortridge (1942) and Roberts (1951), *Eremitalpa* feeds mainly on various sand-burrowing lizards; Holm (1969) mentions also termites, ants and tenebrionid larvae.

Because of the experimental difficulties of observing underground locomotion, the digging of *E. granti namibensis* is poorly known. Holm (1969) studied the movements of the body during underground locomotion by means of a glass terrarium, reporting that the whole digging movement consists of two phases: 'digging with front claws' and 'head and shoulders pressing forwards and upwards'. Puttick & Jarvis (1977), using radiographs in rapid succession, described the alternate movements (power stroke and recovery) of the forelimbs of *Chrysochloris asiatica* put in a tube filled loosely with sawdust. None of these experimental studies was similar enough to the natural conditions to reach a good knowledge of the morphofunctional characteristics during locomotion in sand. The serial photographical technique (six frames/sec) provided ten times less information than cinefluorography (64 frames/sec).

From a morphological viewpoint, the detailed anatomy of *E. granti namibensis* is still poorly known. Among chrysochlorids, *Chrysochloris* has been described in detail by Dobson (1882) in *A monograph of insectivores*. The adaptive morphological specializations of *Chrysochloris* for digging, which are different from those of the talpids (Yalden, 1966), but similar to those of the marsupial mole *Notoryctes* (Stirling, 1891), have been studied by Puttick & Jarvis (1977).

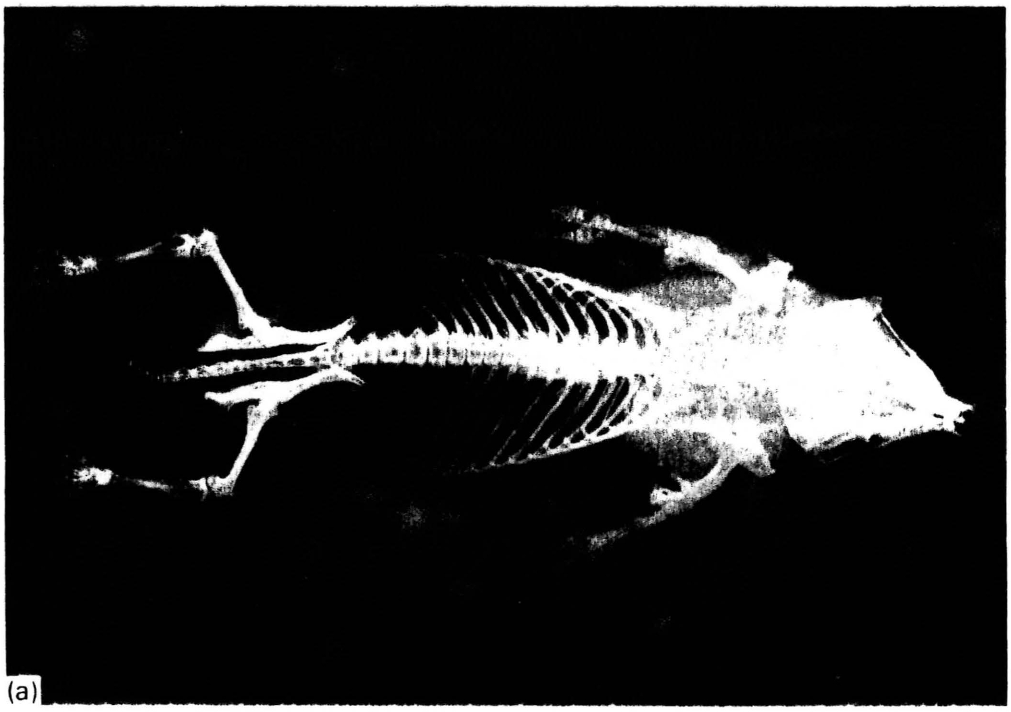
Eremitalpa granti namibensis is small (≃ 80 mm in length, 35 g in weight). The general body shape is elliptical as seen from above, and biconvex transversely: 'roundly oval like a small tortoise' (Walker, Warnick, Hamlet, Lange, Davis, Uible & Wright, 1968). The rostral end is ventrodorsally flattened and spade-shaped. There are neither visible eyes, nor external ears. The mouth is located ventrally. Forelimbs are parasagittally oriented; the thighs are transverse. The powerful hands have four digits with strong claws; the feet have five toes of moderate size (Plate I(a)).

The Namib Golden mole differs from the Cape Golden mole in many myological features which, until now, have not been systematically described, although they may be considered in relation to the particular mode of digging.

In order to evaluate the adaptive relationships between the peculiar morphology of the locomotor system of *E. granti namibensis*, the digging locomotion, and the soil mechanical characteristics of the dune sand, we have carried out a morphofunctional study using a cinefluorographical technique for analysing the movements, and radiographical techniques and dissections for studying the osteology and myology of the locomotor system.

Material and methods

Four specimens of *E. granti namibensis* were provided by the Mission Coineau's expeditions to Namibia (1981 and 1982). Two of them died in transit. Radiographs were taken and both animals were dissected. Two others stayed alive during 7 months and were subjects of several cinefluorographical experiments.



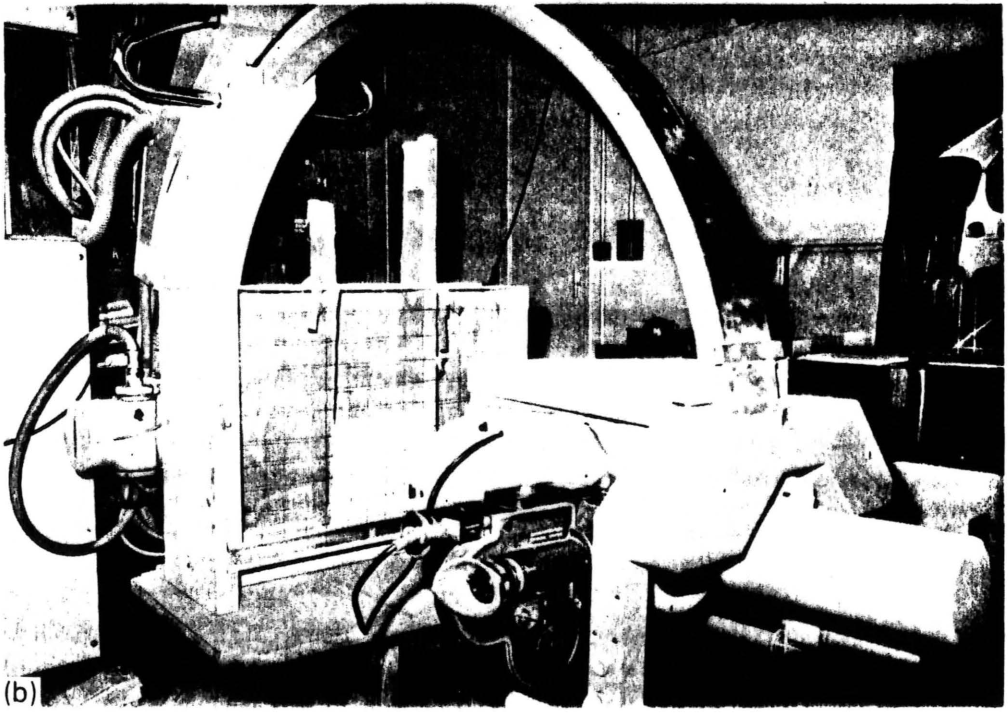


PLATE I. (a) Radiograph of *Eremitalpa granti namibensis* from a dorsoventral incidence. (b) Photograph of the cinefluorographic system.

Cinefluorographic experiments were carried out with a Massiot Medio Philips X-ray generator according to the technique described by Jouffroy & Gasc (1974).

Though the animals arrived in France in a container filled with dune sand of the Namib Desert, we had to find a sand-like substratum characterized by its transparency for X-rays. After several unsuccessful attempts, the finest available type of semolina (grain size ≃ ½ mm) appeared to be the most suitable medium. A glass terrarium 55 × 42 × 48 cm was filled with this substitute sand, hereafter called 'sand' for simplicity. One of the glass sides was lined with a metal net of rectangular 4 cm mesh to provide a spatial reference (Plate I(b)).

Several series of experiments were carried out with the 2 individuals and recorded with a 16 mm Arriflex cinecamera and with a video camera (Plumbicon). The total of all recordings amount to 20 min of film and tape 3/4". From all the records, we selected the clearest episodes showing the animal either in lateral or dorso-ventral views.

These episodes were analysed by means of a motion analysis projector SPECTO MK3, and by superimposing the successive frames on a screen covered with tracing paper.

In addition to the skeletal elements of the body, hollows between the body and the sand are visible.

For the graphic analysis of the force system, we studied X-ray motion pictures in lateral view only because the head and forelimb movements are mainly achieved in parasagittal planes, and most of the muscles involved are themselves oriented in such planes.

A good knowledge of morphology from dissection and the use for control of the radiographs permitted us to recognize muscular insertion sites on the different bones and to plot them on the cinefilm pictures with a satisfactory accuracy, despite the small size of the Namib Golden mole. With few specimens, dead ones were carefully dissected (myological terminology according to Jouffroy, 1971).

For graphic analysis, the same length was given to all vectors, focusing interpretation on the lines of action of forces, values or arm levers, and effect of torques.

Results

Cinefluorographical analysis of the movements

We identified two kinematic patterns of burrowing locomotion: 1) an 'initial penetration' pattern, when the animal penetrates the sand from the surface; and 2) a 'progression' pattern, when the animal moves forward while totally buried below the surface.

Initial penetration pattern

In all sequences studied, the animal immediately plunges its head vertically into the 'sand' when put on the surface. Both hands are successively introduced into the sand just beneath the throat to initiate the digging parasagittal movements ('terrier' model, Reed, 1951). The body is firmly bent ventrally and pushed downwards by the extension of the hind limbs from the feet resting on the surface.

When completely buried, the animal continues moving obliquely downwards, using for a short while the locomotor pattern that was described by Puttick & Jarvis (1977), which is different from the typical progressing pattern that we describe later.

The forelimbs and hind limbs are out of phase. The head is bent dorsally while the forelimbs are symmetrically retracted backwards; the animal 'opens' its path. Simultaneously, the hind limbs are protracted under the belly.

Underground progressing pattern

As the pathway becomes more and more difficult to open, due to the increasing resistance of the more compact sand, both pairs of limbs progressively come to move in phase. A complete

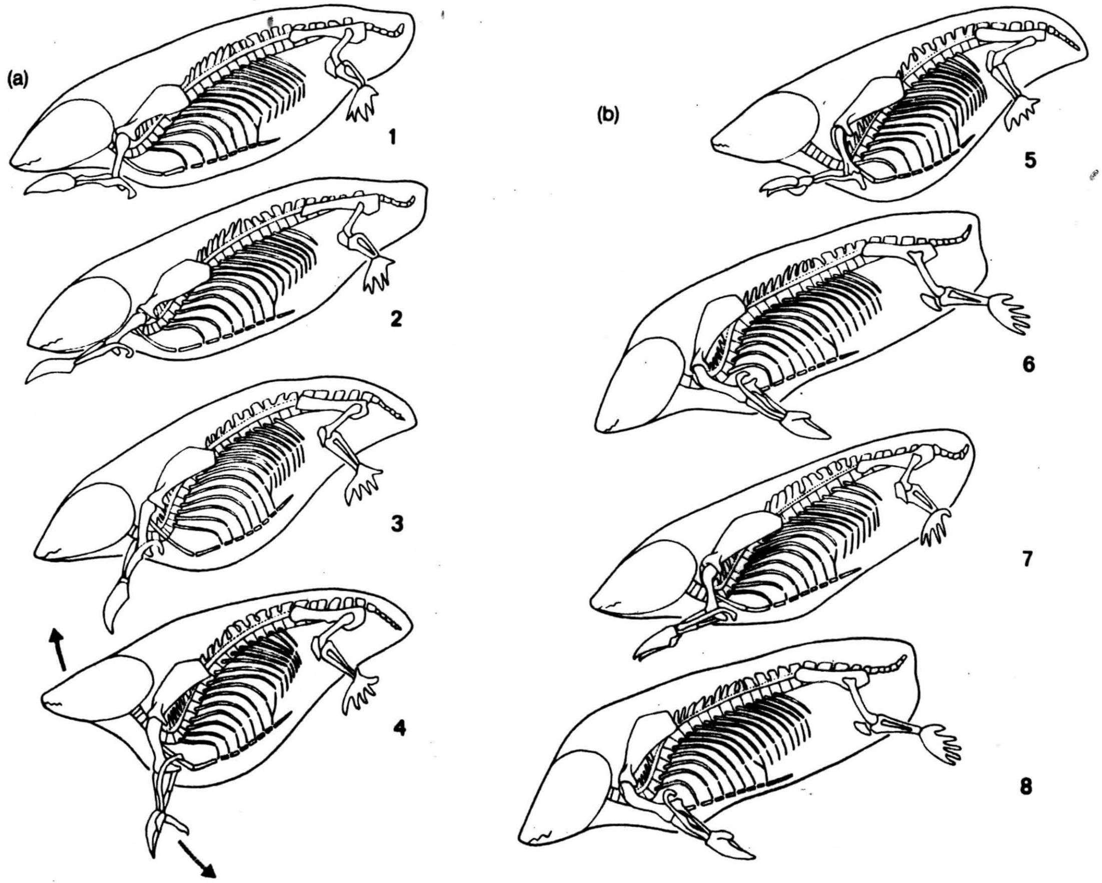


FIG. 1. Schematic drawings of: (a) buttressing phase and (b) digging-propulsion phase from X-ray cinematography. 1-8: see text.

cycle is made up of one 'buttressing' phase followed by several (2–5) 'digging-propulsion' phases.

During the buttressing phase (Fig. 1(a)), the animal is supported by its four hands and feet, while simultaneously employing a dorsiflexion and uprising of the head and the extension of forelimbs. The hands are firmly anchored in the sand in a pronated position, with the first finger abducted backwards.

Lateral X-ray views reveal that, in this position, the forearm is made of three parallel bony structures: besides the radius and the ulna, there is a third long bone, the 'flexor bone' (see below, musculature and Fig. 3). When the forelimbs are fully extended, the humeri are medially rotated and the pectoral girdles are strongly protracted, so that the scapulo-humeral joint comes to be located in the same transverse plane as the cranio-cervical joint. The dorsal aspect of the head is brought parallel to the frontal plane by a dorsi-flexion of the cervical column (Fig. 1(a), 4). The feet bury themselves deeper in the sand as the posterior part of the body lowers, in reaction to the uprising of the anterior part. A slight flexion of the hip and knee joints occurs.

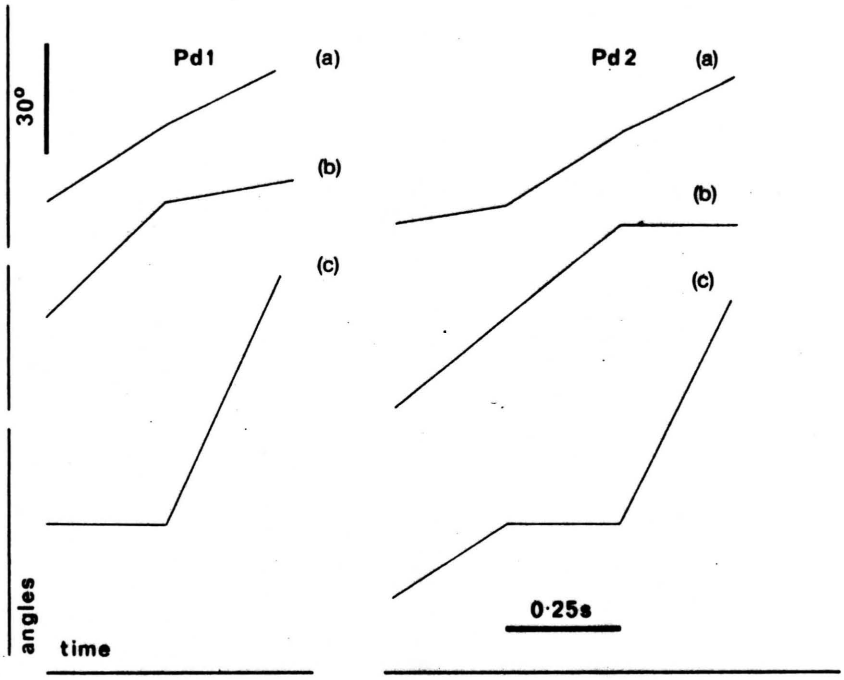


FIG. 2. Angular rotation of three segments of the forelimb articulatory chain during iterative propulsion digging phases. Two episodes (Pd1 and Pd2) are represented to point out the consistency of the movement. (a) angular rotation of the scapula; (b) rotation of the humerus in relation to the scapula; (c) rotation of the ulna in relation to the humerus.

This buttressing movement results in a compression of the surrounding sand, especially above and behind the backward sloped dorsal surface of the body; simultaneously, a depression is produced just in front of the chest, with a hollow volume between the head and the claws. The buttressing phase is short: lasting an average of about 200 or 300 msec, but the animal may keep the most extreme extended position for several seconds.

During the digging-propulsion (iterative) phase (Fig. 1(b)), the forelimbs, leaving their support, are flexed and protracted while the body is supported by the hind limbs. The claws penetrate the sand beneath the chin. The scapulo-humeral joint is moved backwards to the level of the first thoracic vertebra, and dorsally elevated (Fig. 1(b), 5). Simultaneously, the dorsiflexion of the cranio-cervical system diminishes slightly. At a normal speed of the camera (24 frames/sec), the hands seem to move symmetrically, but sequences recorded at 64 and 80 frames/sec reveal that one of the hands is in advance of the other. When both hands have reached pre-digging position beneath the chin, digging begins by synchronous movements of both forelimbs, i.e. shoulder extension (limb retraction) and elbow extension (Fig. 1(b), 6). The sand collected by scratching beneath the chin is pushed back under the belly by a powerful terminal thrust of both hands. Pictures from above show that the hands are close to the mid-ventral line at the end of the movement. The parasagittal movement of *Eremitalpa*'s forelimbs characterizes this digging mechanism in contrast to the transverse talpid model (Yalden, 1966).

Each segment of the forelimb acts differently in the backward motion of the whole. Plotting the angular displacements of the scapula, the humerus and the forearm (Fig. 2), three periods are recognized. First, the scapula is rather still, the general limb retraction is performed mainly by the humerus, together with the extension of the elbow. Secondly, no motion occurs in the elbow, while the scapula and the humerus move. Lastly, the main motion is provided by the elbow extension, whereas the two other segments are relatively still.

When the retracting forearm becomes parallel to the tibia the hind limbs begin to extend with a backward displacement of the feet: from this moment onwards, the four limbs move synchronously so that the final thrust is due to the cooperation of the four limbs. It provokes, by reaction from the sand, a forward progression of the body and a penetration of the rostrum of the head into the sand, while the cervical column straightens. At the end of the thrust, the animal is stopped in a static balance (Fig. 1(b), 6): for progressing further, another 'digging-propulsion' phase is required. Each of the feet takes a step, while the dorsal part of the vertebral column extends to secure the rostral pressure against the sand. The forelimbs flex again and the claws are brought forward beneath the chin (Fig. 1(b), 7). The return movement to the pre-digging position lasts about 150 ms; it is followed by a new digging propulsion cycle (Fig. 1(b), 7–8).

Two to five digging-propulsion phases may be performed successively until a new compression by buttressing is needed.

Comparison of different experiments shows that the physical characteristics of the sand and the depth reached by the animal have an effect on the duration and the timing of the cycle, but do not modify the sequential order of its phases.

Morphology of the locomotor system

Skeleton (Plate I(a) and Figs 3 and 4)

The most characteristic features of the skull of the Namib Golden mole have been described mostly from a taxonomic point of view (Cooper, 1928; Roux, 1947; Simonetta, 1956, 1957*a*, *b*, 1968). These authors have shown that the shape and size of the malleus affect not only the morphology and the connections of the bones of the temporal region, but also the morphology of the snout (total elongation and shape of the palate) and the occipital region.

The vertebral formula is: $7C+16T+3L+(2+3)S+9Ca$.

The cervical part of the vertebral column shows a dorsally concave curvature. Among thoracic vertebrae, the first eight bear ribs which contact with six sternebrae. There are eight floating ribs. The spines of the first 12 thoracic vertebrae (T1–T12) are perpendicular to the axis of the vertebral column; the spines of T16 and the three lumbar vertebrae are, like those of the first thoracic ones, caudally oriented. The length of the transverse apophyses of the caudal vertebrae increases from Ca2 to Ca4 and decreases from Ca4 distalwards.

The most striking features of the appendicular skeleton are to be found in the pectoral girdle and forelimbs. The pectoral girdle is made up of two narrow scapulae which are elongated parallel to the spine, the distal third of which has a long metacromion. The orientation of the scapulae (axes of their spines) is approximately parallel to the anterior part of the thoracic vertebral column, so that the so-called 'medial border' is here caudally oriented. The entire pectoral girdle is located very anteriorly so that the shoulders are in the same transverse plane as the posterior part of the skull (Plate I(a)). The clavicles are elongated and unusually slender. Proximally, they articulate with the rod-like manubrium, which is prolonged caudally by six sternebrae and the xiphisternum. The length of the manubrium is equal to the lengths of the three first thoracic vertebrae. The clavicles do not present any sigmoid curves, but a unique dorsally concave curvature, laterally passing around in front of the humeral diaphysis before joining the acromio-clavicular joint

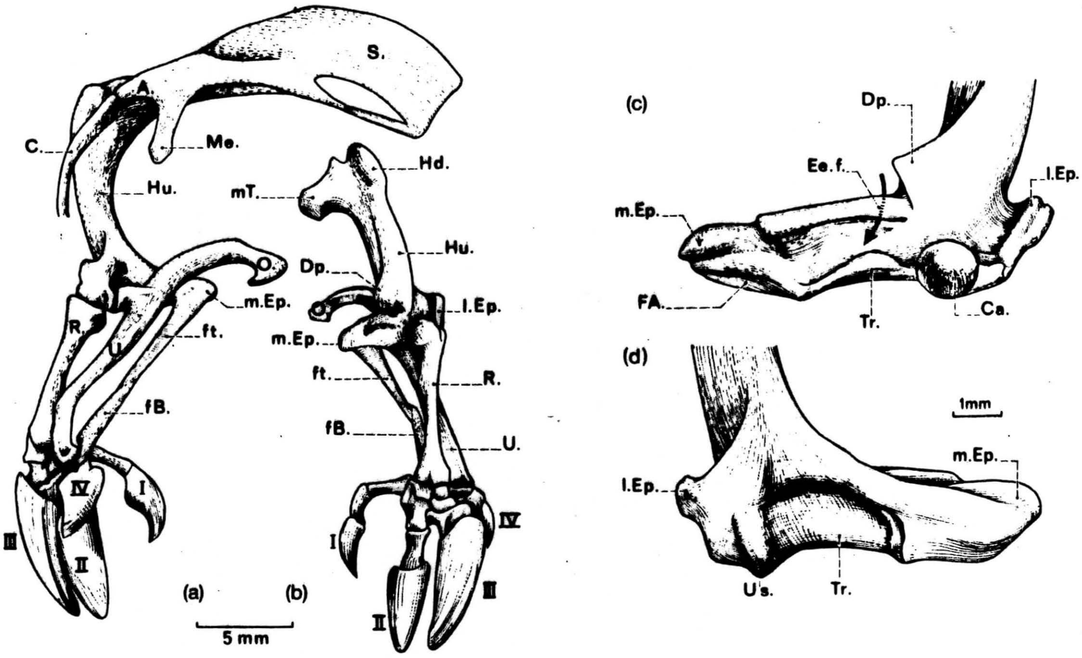


FIG. 3. Skeleton of the left forelimb. (a) lateral view; (b) dorsal view; (c) anterior view of the distal epiphysis of the humerus; (d) posterior view of the distal epiphysis of the humerus. A., acromion process; C., clavicle; Ca., capitulum; Dp., delto-pectoral ridge; Ee.f., entepicondylar foramen; FA., origin area of the flexor tendon; fB., flexor bone; ft., flexor tendon; Hd., humeral head; Hu., humerus; l.Ep., lateral epicondyle; Me., metacromion process; m.Ep., medial epicondyle; mT., medial tuberosity; O., olecranon process; R., radius; S., scapula; Tr., trochlea; U., ulna; Us., humero-ulnar stop; I to IV, finger claws.

(Fig. 3(a)). The head of the humerus is elliptical and very narrow. The upper extremity of the humerus is strongly dissymmetrical due to the unusual shape and size of the 'lesser' tuberosity which protrudes far from the medial side of the humerus (Fig. 3(b)). The humeral shaft is markedly curved, i.e. posteriorly concave. The torsion of the humeral shaft averages 120°; the trochlear axis of the elbow is obliquely oriented: medially and backwards, laterally and forwards.

The delto-pectoral crest extends to the distal part of the shaft, ending in a rough process which overlaps the capitulum (Fig. 3(c)). The entepicondylar foramen allows the median nerve to pass into the antebrachium. The lower extremity of the humerus (Fig. 3, (c), (d)) is strongly asymmetrical; the capitulum is located approximately on the axis of the shaft, while the wide trochlea protrudes medially so that the groove is located far from the axis of the diaphysis. The medial epicondyle is very protuberant; the total width of the distal epiphyses amounts to 65 % of the total length of the humerus.

The forearm is made up of three bones: ulna, radius and 'flexor bone' (Fig. 3(a)). The upper extremity of the ulna has a very long, robust, crook-shaped olecranon, which juts out medialwards and bends ventrally. The trochlear notch constitutes a deep socket articulating with the groove of the humeral trochlea. A crest, which runs on the lateral border of the notch, articulates with a bony process of the posterior part of the humeral trochlea (Fig. 3(d)).

The upper extremity of the radius is cup-shaped and articulates with the spherical capitulum of the humerus. In the distal part of the radial shaft, on ventral aspect, there is a process under which the tendon of the m. flexor carpi radialis passes before proceeding to its insertion (see below). The diaphysis of the radius crosses over the diaphysis of the ulna; the forearm is strongly pronated.

The third bone (flexor bone) appears to be an ossification of the flexor tendon, a feature characteristic of the chrysochlorids (Flower, 1876; Macalister, 1878; Dobson, 1882; Hildebrand, 1974; Puttick & Jarvis, 1977). The length of the flexor bone equals two thirds of the radius; it extends along the distal third of the ulna to the carpus, and is therefore much shorter than in the Cape Golden mole *Chrysochloris asiatica* (Puttick & Jarvis, 1977).

The wrist is highly modified: carpals and metacarpals are more or less fused and impossible to identify and homologize with adult hands. Kindahl (1949) untangled the puzzling problem of bone knitting by studying the morphogenesis of the hand of *Eremitalpa granti* in five stages of embryonic development (from 9 mm to 25 mm) and in adults. We will refer to Kindahl (1949) to describe the most important features of the hand skeleton in relation to locomotion.

The four fingers are the four radial ones (I to IV)—the fifth one fails to develop in the early stages of the ontogenetic process. The hand is definitely mesaxonic: the third digit is by far the longest and the most powerful; its axis prolongs the forearm.

The carpus comprises eight bones (Fig. 4 (a), (b)); there is no centrale. The wide distal epiphysis of the radius articulates with the scaphoid and the lunate, the epiphysis of the ulna with the triquetrum and the pisiform. In the first row of carpals, scaphoid, lunate and triquetrum are placed side by side. In the second row, trapezium, trapezoideum, os magnum and unciformis are firmly engaged into one another.

Distally, along the axis of the hand, the lunate articulates with the os magnum, and the os magnum with a huge bony structure which results from the fusion of the third metacarpal with the first and second phalanges of the third finger (Kindahl, 1949). The third phalanx is hyperdeveloped, very long, bifid and equipped with an enormous claw. On the dorsal aspect of the fused bone, a hollow articulates with a smooth relief of the basis of the third phalanx, limiting the dorsi-flexion of the latter.

On the radial side of the morphological axis of the hand, the second finger is made up of two bones, the proximal resulting from the union of the two first phalanges. The distal phalanx is bifid. The second metacarpal is fused with the trapezium and the trapezoid. The second finger, though smaller and shorter than the third, is still very powerful. The first finger consists of three bones, the first metacarpal and two phalanges. The first metacarpal articulates on the medial aspect of that bone which results from the knitting of the trapezium, trapezoid and second metacarpal. The distal phalanx is not bifid and wears a claw. The orientation of the thumb is unusual in so far as the axis of the first metacarpal is perpendicular to the axis of the hand: we have seen that the thumbs are strongly abducted during the 'buttressing phase' of locomotion. The distal end of the flexor bone is connected to the basis of the first metacarpal by a strong transverse ligament.

On the ulnar side of the axis of the hand, the fourth digit is made up of a very short metacarpal and two bones; the more proximal of the latter resulting from the fusion of the first two phalanges. The fourth metacarpal, which looks like a carpal (Fig. 4), articulates on the hamatum. The distal phalanx is bifid and wears a claw.

Musculature (Figs 5 and 6)

The Namib Golden mole, like other chrysochlorids (Jullien, 1967), differs from the insectivoran pattern in several myological features of the pectoral girdle and the forelimb which are related to the peculiar mode of locomotion of these animals.

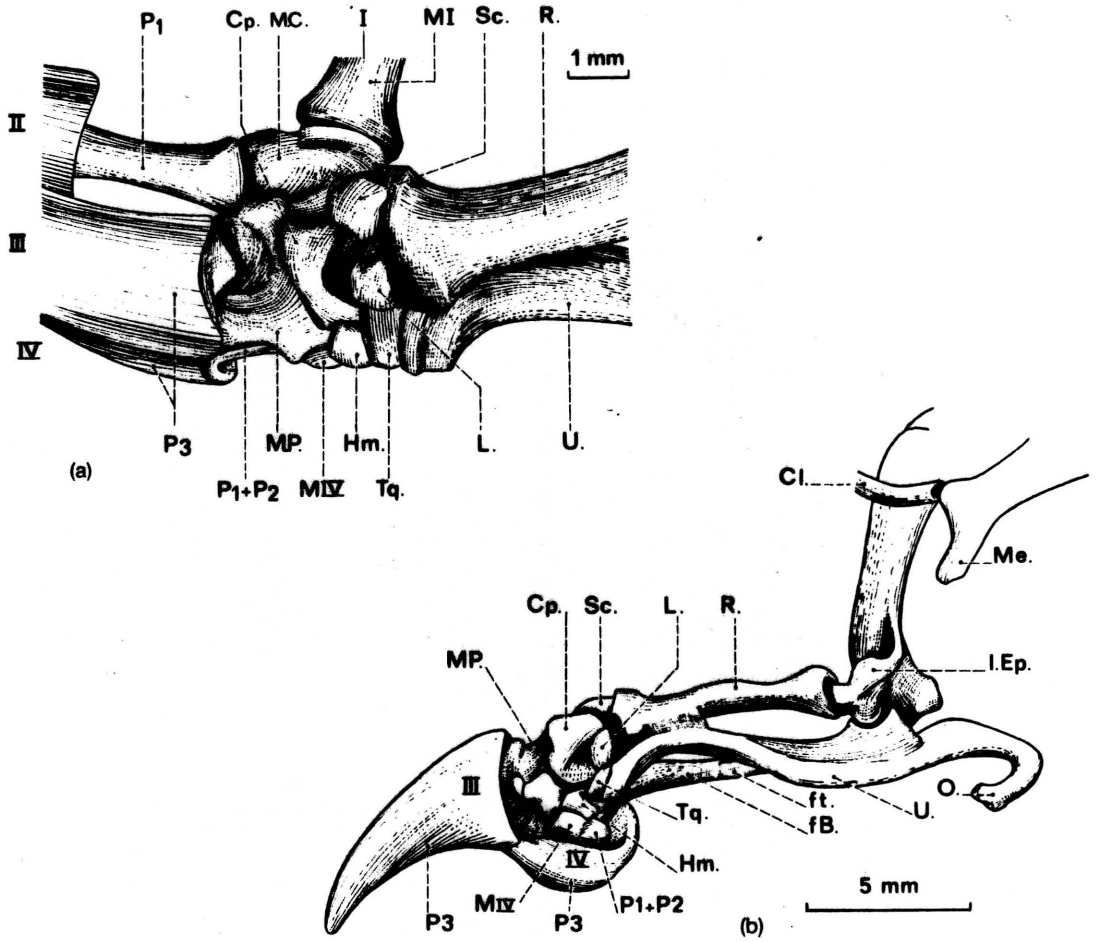


FIG. 4. Left forelimb: (a) medio-dorsal view of the carpal region; (b) lateral view of the forearm and carpus. Cl., clavicle; Cp., capitate; fB., flexor bone; ft., flexor tendon; Hm., hamate; l.Ep., lateral epicondyle; L., lunate; M I to M IV, metacarpals 4; M.C., fused trapezium + trapezoid + metacarpal II; Me., metacromion process; MP., fused metacarpal + phalanges 1 and 2 of the third digit; O., olecranon process; P1 to P3, phalanges; R., radius; Sc., scaphoid; Tq., triquetrum; U., ulna; I to IV, digits.

1. Muscles between the pectoral girdle and the occipital region of the skull are very powerful; contrastingly, most muscles connecting the cervico-thoracic vertebrae to the scapula are either absent or poorly developed. We shall consider, successively, dorsal and ventral aspects of the body.

Dorsally (Fig. 5(a)), musculus trapezius does not originate from the cervical and thoracic vertebrae. It is made up of two parts. Pars anterior consists of a wide trapezoidal muscular sheet, originating from the entire occipital crest between the mastoid processes, and inserting on the spines of the scapulae. Musculus trapezius extends from the metacromion, ventrally, to the vertebral border, dorsally. This pars anterior looks like a cowl ('cucullaris', or cape), spreading out

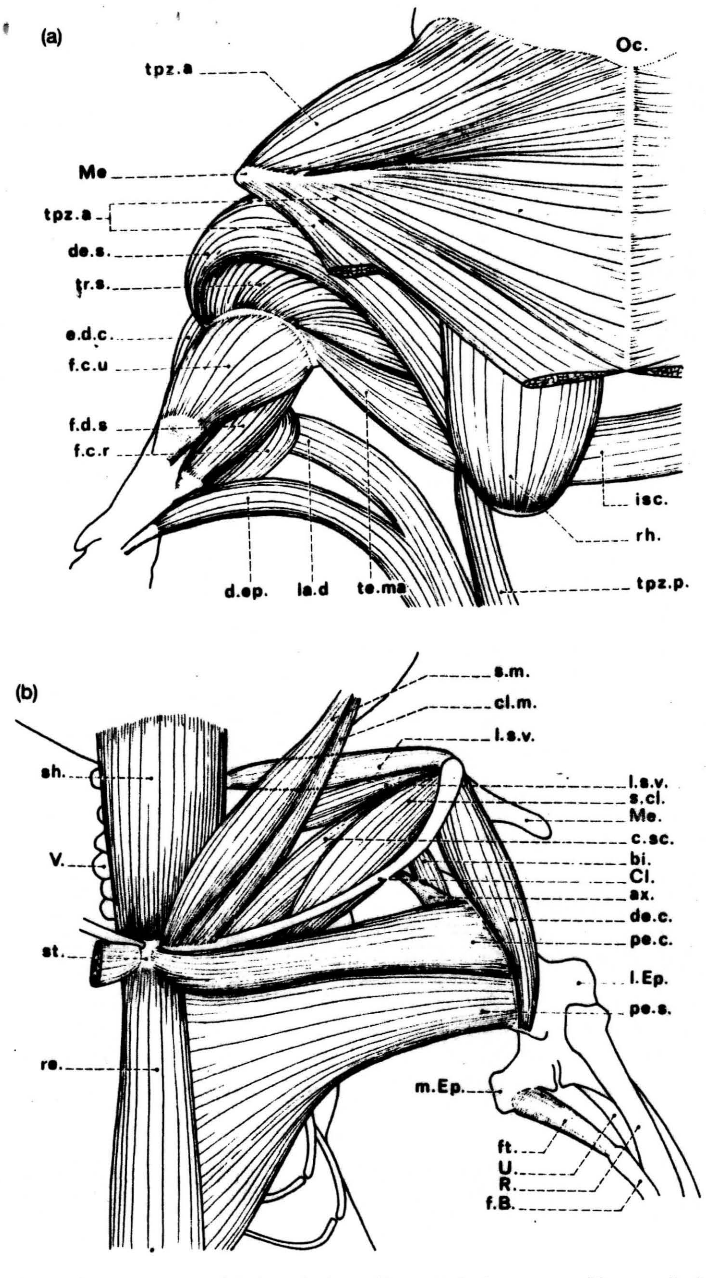


FIG. 5. Left shoulder and arm muscles. (a) dorsal view; (b) ventral view. ax., axillary arch; bi., biceps brachii; Cl., clavicle; cl.m., cleido-mastoideus; c.sc., costo-scapularis; de.c., deltoideus pars clavicularis; d.ep., dorso-epitrochlearis; de.s., deltoideus pars scapularis; e.d.c., extensor digitorum communis; f.B., flexor bone; f.c.r., flexor carpi radialis; f.c.u., flexor carpi ulnaris; f.d.s., flexor digitorum superficialis; ft., flexor tendon; isc., interscapularis; la.d, latissimus dorsi; l.Ep., lateral epicondyle; l.s.v., levator scapulae ventralis; Me., metacromion process; m.Ep., medial epicondyle; Oc., occipital bone; pe.c., pectoralis pars clavicularis; pe.s., pectoralis pars sternalis; R., radius; re., rectus abdominis; rh., rhomboideus pars occipitalis and pars cervicalis; s.cl., subclavius; sh., sterno-hyoideus; s.m., sterno-mastoideus; st., sternum; te.ma, teres major; tpz.a, trapezius pars anterior; tpz.p., trapezius pars posterior; tr.s., triceps pars scapularis; U., ulna; V., cervical vertebrae.

from the skull to the tips of both shoulders, without any connection with the vertebrae. Pars posterior consists of a narrow muscular strip originating from the lumbar fascia and the spines of the vertebra T12 to L2, and inserting on the spine of the scapula, near the medial border (which is here caudally oriented); contraction results in a caudal displacement (retraction) of the scapula.

Musculus rhomboideus also does not insert on the thoracic vertebrae, and comprises three parts: pars occipitalis, pars cervicalis and pars interscapularis. Pars occipitalis and pars cervicalis arise, respectively, from the occipital bone and from the cervical fascia, close to the skull, but not from any of the cervical vertebrae. Both parts are in the same layer, the direction of their fibres lying parallel to the axis of the body. They both insert on the medial (here caudal) border of the scapula: pars cervicalis inserts more medially on the medio-caudal angle, and pars occipitalis more laterally along the entire border. According to the direction of their fibres, these two parts are powerful extensors of the head.

Pars interscapularis is an unpaired muscle which consists of transverse fibres joining up the medio-caudal angles of both scapulae; contraction results in the adduction of the scapulae toward the axis of the body. Pars interscapularis has already been described in other chrysochlorids (Dobson, 1882) and talpids (Yalden, 1966).

Musculus serratus magnus is the only dorsal muscular connection between the pectoral girdle and the cervical column, arising from the transverse processes of the last five cervical vertebrae (by separate digitations) and inserting on the medial (here caudal) border of the scapula.

The digitation originating from the third cervical vertebra separates from the serratus magnus and inserts on the medial border of the scapula (see below levator scapulae dorsalis).

Ventrally (Fig. 5(b)), m. sternomastoideus and m. cleido-mastoideus arise from the tip of the manubrium sterni and from the extreme medial part of the clavicle, respectively; their insertions are upon the mastoid process of the temporal bone, and, according to the direction of fibres, both are powerful flexors of the head.

Four muscles link up rather transversely and obliquely the shoulder to the axial skeleton, occurring successively in the cranio-caudal direction (Fig. 9): first, m. levator scapulae ventralis is made of two bundles (levator scapulae + levator clavicular (Dobson, 1882–1892)); it originates from the transverse processes of the first and the third cervical vertebrae; both parts insert on the spine of the scapula caudally to the basis of the metacromion. Secondly, m. levator scapulae dorsalis connects the transverse process of the third cervical vertebra and the spine of the scapula. Thirdly, m. subclavius arises from the ventral border of the sternum, crossing under the clavicle and passing along the ventral surface to insert into the distal end and on the acromion. Fourthly, m. costo-scapularis arises from the two first costal cartilages and inserts into the acromion. Musculus costo-scapularis abuts on the subclavius but does not insert into the clavicle.

These four muscles, like m. trapezius dorsally, make up a muscular webbing which reinforces cohesion of the pectoral girdle.

2. Insertions of most muscles connecting the body, or the scapula, to the forelimb are much more distally located than in the general mammalian pattern. Consequently, the lever arms of these muscles are longer, and the muscles more powerful at the expense of the amplitude of angular movement of the bones.

Musculus latissimus dorsi, originating from T11 to L3 vertebrae, inserts into the medial epicondyle of the humerus (instead of the upper part of the shaft). Musculus dorsoepitrochlearis, which splits off from m. latissimus dorsi, inserts into the distal part of the diaphysis of the radius (instead of the olecranon). The powerful m. teres major inserts into the olecranon, beside m. triceps (instead of the upper part of the shaft of the humerus). Musculus deltoideus, which is made up of two parts, scapularis (Fig. 5(a)) and clavicularis (Fig. 5(b)), inserts into the distal extremity of the shaft of the humerus, into the deltoid ridge that overhangs the capitulum of the humerus (instead of the middle of the shaft).

Ventrally, m. pectoralis major (pe.s., Fig. 5(b)) inserts into the deltoid ridge near the capitulum (instead of the middle third of the shaft).

3. There is a striking disparity in the development of antagonistic groups of muscles.

Among muscles of the shoulder-joint, the medial rotator is powerful, and the lateral rotator is weak. The powerful m. subscapularis inserts into the tip of the protruding lesser tuberosity (see above); the torque resulting from its isotonic or isometric contraction is increased by the unusually great length of the power arm. Musculus infraspinatus, like m. supraspinatus, is very weak and inserts on the greater tuberosity.

Among muscles of the elbow joint, flexors are weak and extensors are powerful. Musculus biceps has only one head, originating from the supraglenoid tuberosity of the scapula. Musculus brachialis is absent. The different heads of musculus triceps are bulky; an increased efficiency of the extensor group is due to the great length of the olecranon process on which they insert.

Among muscles of the wrist and of the fingers, extensor muscles are weak and flexors are overdeveloped. The extensors are six in number (Fig. 6(a)): abductor pollicis longus, extensor digitorum communis, extensor carpi ulnaris, extensor carpi radialis, extensor profundus and extensor lateralis. The first four muscles originate from the lateral epicondyle of the humerus, the last one from the olecranon; all except m. extensor digitorum superficialis are weak and slender.

The flexor muscles (Fig. 10(b)) are five in number. 1) Musculus flexor carpi ulnaris originates from the olecranon and inserts on the ulnar carpale. 2) Musculus flexor digitorum superficialis, which is very weak, lies upon the musculus flexor digitorum profundus; it originates from the medial epicondyle of the humerus and ends on a transverse ligament of the wrist. 3) Musculus flexor digitorum profundus, which is extremely bulky, originates from the medial epicondyle of the humerus by means of a tendinous raphe, and from the olecranon by muscular fibres. In the first third of the forearm, the raphe turns into a bony structure which looks like a third bone of the forearm (Fig. 6(b)). At the level of the wrist, this flexor bone is bound to the bases of metacarpals I and IV by means of two oblique ligaments. Distally, it turns into fibre bundles which insert on the bases of the first phalanges of the fingers II, III and IV. 4) Musculus flexor carpi radialis is a very thick muscle, originating on the medial epicondyle of the humerus and inserting into the palmar side of the trapezium. 5) Musculus pronator teres radii originates from the medial epicondyle and inserts into the middle third of the shaft of the radius.

4. There are no short muscles of the hand except a thin triangular muscular sheet binding metacarpals I and II which is very likely a remnant of the m. contrahentes layer (adductor hallucis brevis, caput transversum).

Discussion: biomechanical interpretation

In order to untangle the relationships between form and function, it is necessary to analyse the biomechanics of the system. In the following discussion, we attempted to reconstruct the dynamic conditions during the different phases of locomotion. Since the actual magnitude of forces was not available, we focused on their lines of action (Fig. 7), with the arbitrary assumption that the forces are all of the same magnitude (Govaerts, 1962). On the sagittal X-ray motion pictures, we considered the lines of action joining the centroids of muscle attachments. Since the limbs move in

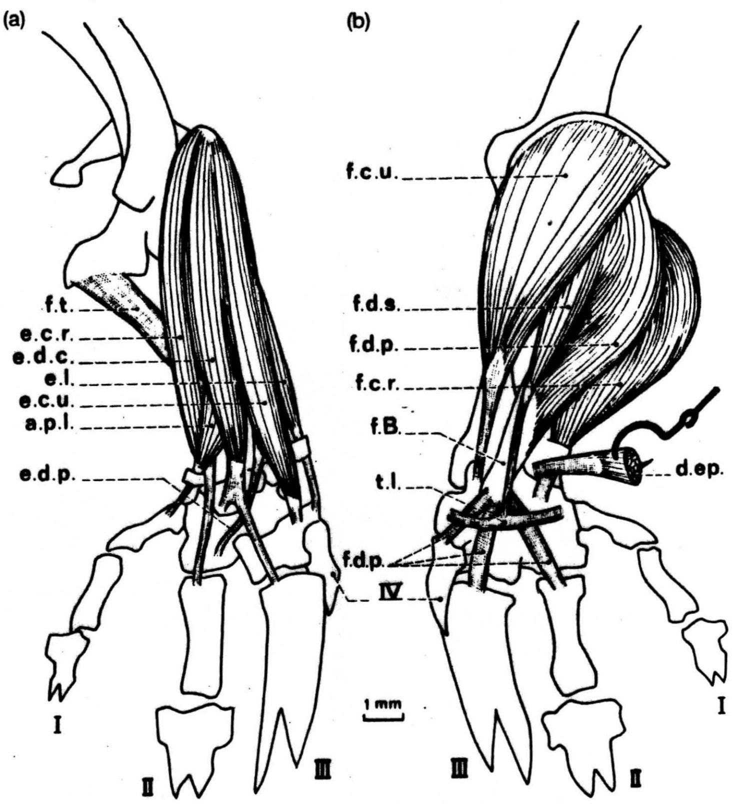


FIG. 6. Left forearm muscles: (a) anterior view; (b) posterior view. a.p.l., abductor pollicis longus; e.c.r., extensor carpi radialis; e.d.c., extensor digitorum communis; e.d.p., extensor digitorum profundus; e.l., extensor lateralis; f.t., flexor tendon; f.B., flexor bone; f.c.r., flexor carpi radialis; f.c.u., flexor carpi ulnaris; f.d.p., flexor digitorum profundus; f.d.s., flexor digitorum superficialis; t.l., transversal ligament of the wrist (flexor retinaculum); d.ep., dorso-epitrochlearis. I to IV, digits.

a parasagittal plane, measurements of length variations between origin and insertion centroids provided us with a suitable approximation of the muscular action.

Given the confusing ambiguity in the morphofunctional terminology of locomotion, it must be specified that the terms 'extension' and 'flexion' are used in this paper to describe the movements of the joints (shoulder, elbow . . .), whereas the global forth and back movements of the limbs in parasagittal planes are described as 'protraction' and 'retraction'.

'Rotation' means any movements of a joint in relation to every axis passing through its centre (mechanical acceptation). In Figs 8 to 12, the bone lines are mechanical, not anatomical, axes.

Buttressing phase (Figs 8 to 10)

Each cycle begins at the end of a propulsion phase, when the animal meets with such a sand resistance at the level of the snout and maximum body width ('midship frame') that it becomes necessary to open up the sand lying in front of the head. To achieve this, the mole exerts a double thrust against the sand: first, along the top of the head and the cervico-thoracic part of the back,

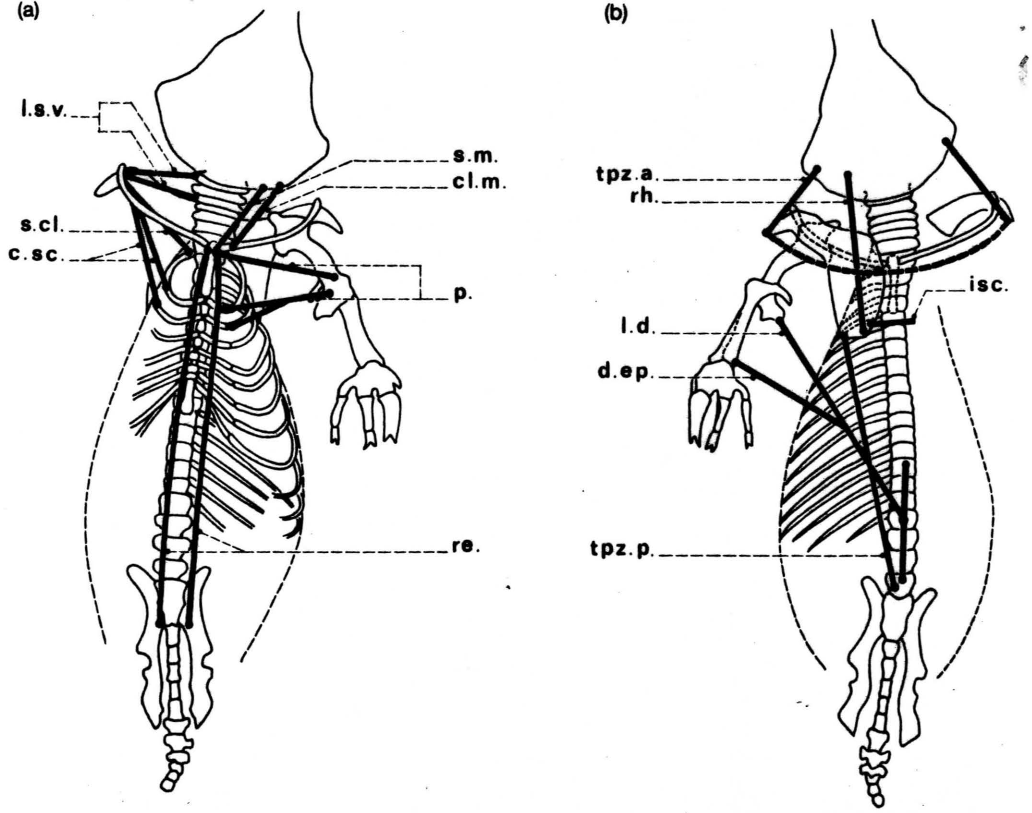


FIG. 7. Simplified representation of the muscle of the head-and-pectoral-girdle system (from radiographs). (a) Ventral view; (b) dorsal view. cl.m., cleido-mastoideus; c.sc., costo-scapularis; isc., interscapularis; l.s.v., levator scapulae ventralis; re., rectus abdominis; rh., rhomboideus; l.d., latissimus dorsi; d.ep., dorso-epitrochlearis; p., p. occipitalis and p. cervicalis; s.cl., subclavius; s.m., sterno-mastoideus; tpz.a., trapezius, pars anterior; tpz.p., trapezius, pars posterior.

and secondly, along the chest. The compactness of the sand (spatial arrangement of particles) is modified by this pressure, resulting in an open space, filled by the extracted air, which appears between the chin and hands.

The buttressing phase may be divided (see above) into two subphases characterized by simultaneous movements of the forelimbs: first, forward extension of the forelimbs (shoulder flexion) and secondly backward retraction of the extended forelimb (shoulder extension).

Subphase 1

The first subphase begins with a flexion of the shoulder (forward swing of the humerus in a parasagittal plane amounting to about 40°), accompanied by extension of the elbow, bringing the orearm and the hand along the chin and thorax (Fig. 8(a)). The head shows a slight ventral lexion, while the ventral curvature (dorsally concave) of the cervical column increases.

Musculi trapezius p. anterior and p. posterior, rhomboideus p. occipitalis and p. cervicis, iceps p. scapularis and teres major do not show any length variation. Musculus latissimus dorsi retches slightly and becomes parallel to the scapula-forelimb chain, the elements of which lie

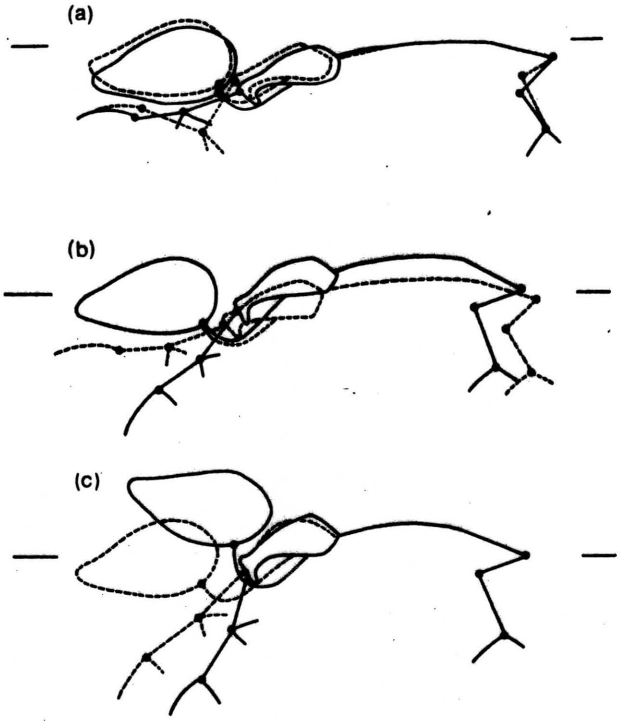


FIG. 8. Diagrammatic representation of the buttressing phase from cinematography. The movement is pictured from dashed to solid outlines. (a) forelimb protraction (shoulder flexion + elbow extension); (b) beginning of the forelimb retraction (shoulder extension); (c) climax of the buttressing phase.

strictly in lines. The elbow extension is not correlated with a significant shortening of the tricipital complex. Figure 12 shows that the combined movement of forward swing of the humerus and of elbow extension is performed without any change in the length of m. teres major and m. triceps (isometric contractions), due to the anatomical feature of a 145° angle between the ulnar shaft and axis of the olecranon process (α, Fig. 9(a)). At the end of subphase 1, the torques of these two muscles are lowest for both shoulder and elbow joints.

Should we take into consideration the resistance met by the claws, the biarticular nature of m. teres major and m. triceps and these torques can be identified as the main factors of the shoulder and elbow combined movement.

Subphase 2

At the beginning of the following subphase, the whole extended limb begins to retract (shoulder extension). Movement of the humerus amounts to about 35°. The hands, with the thumb abducted backwards, are slightly flexed at the wrist joint. The scapula achieves an oblique backward translation (Fig. 8(b)). The dorsal curvature (ventrally concave) of the vertebral column between the cervico-thoracic hinge and the sacrum increases because of the small stride performed by both hind limbs.

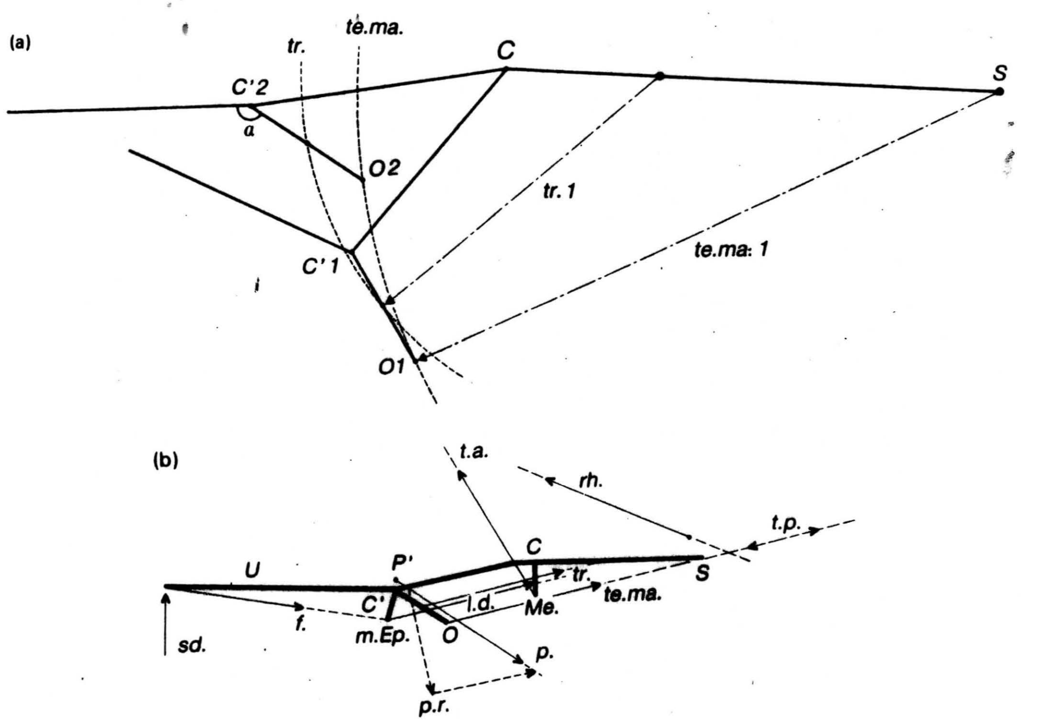


FIG. 9. Diagrammatic representation of some biomechanical parameters at the beginning of buttressing phase (see Fig. 8(a)). (a) Trajectories of the insertions of teres major and triceps muscles, between two stages (1 and 2) of the forelimb protraction (explanations in the text); (b) lines of action of forelimb muscular forces at the beginning of the buttressing phase. Bone lines are mechanical, not anatomical axes: therefore, the insertion *P'* of pectorales on the humerus is slightly apart from *C*-*C'*. *a*, ulnar shaft-olecranon angle; *C*-*C'*, upper arm; *C'*-*O*, olecranon process; *C'*-*U*, forearm; $\vec{f}$., resultant of hand flexor muscles; $\overrightarrow{l.d.}$, latissimus dorsi; *Me.*, metacromion process; *m.Ep.*, medial epicondyle; *O*, tip of the olecranon process; *p.*, pectorales; *P'*, humeral insertion of pectorales; *p.r.*, rotation component of pectorales; $\overrightarrow{rh}$., rhomboideus; *S*-*C*, scapula; $\overrightarrow{sd}$., sand reaction; $\overrightarrow{t.a}$., trapezius, pars anterior; $\overrightarrow{te.ma}$., teres major; $\overrightarrow{t.p}$., trapezius, pars posterior; $\overrightarrow{tr}$., triceps; *U*, ulna.

The pectoral muscles are shortened by about 10 % of their previous length, and from a mechanical point of view are in a position of being the most efficient muscles to retract the humerus. Shortening of the parasagittal components of mm. teres major (12 %) and triceps p. scapularis (8 %) maintains a constant angle between the forearm and humerus despite sand resistance.

At the beginning of this retraction subphase, the graphic analysis of the force system (Fig. 8(b)) shows: First, the starting action of the pectoralis through a strong rotation component in the parasagittal plane (*p.r.*, Fig. 9(b)). Secondly, m. teres major, triceps, latissimus dorsi and the longitudinal component of m. pectoralis only stabilize the scapulo-humeral joint, being more or less parallel to the humeral shaft. Altogether they contribute to push the humeral head into the glenoid fossa, which tends to move the scapula backwards. Since the scapula stands still during this subphase, it may be assumed that the balance is due to the simultaneous activity of two muscular systems 'shrouding' the scapula to the body axis. The first one is made of parasagittal bundles: mm. trapezius p. anterior and p. posterior, rhomboideus p. occipitalis and p. cervicalis and serratus magnus spread, like a fan, all over the costal grid and the cervical column. The second system consists of transversal bundles: dorsally, m. interscapularis links both scapulae to each other and, ventrally, mm. levatores scapulae, dorsalis and ventralis; subclavius and costo-scapularis link the scapula to the body axis (vertebrae, sternum and ribs). This muscular system plays the role of a transverse binding which sets both forelimbs in synchronous motion. Thirdly, both forelimbs stiffen during shoulder extension despite strong resistance of the compacted sand, resulting from a complex mechanism. Obviously, the powerful mm. teres major and triceps extend the elbow, and a functional unit, consisting of the flexor bone-and-tendon and the wrist and hand flexor muscles, prevents the wrist extension that would occur because of the sand pressure against the claws.

When the forearm is fully extended, the protruding medial epicondyle is facing backwards because of the permanent medial rotation of the humerus (along its axis). Consequently, the medial epicondyle provides the hand flexor muscles with a very long lever arm. As with talpids, there is an automatic connection between the medial rotation of the humerus and the palmar flexion of the wrist. The strength of the flexor tendon which is armoured with bone tissue is related to this function. Therefore, the medial rotation of the humerus does help the hand to counterbalance the resistance of the sand.

The forelimbs push strongly against the sand at the end of the shoulder extension. The action of these struts generates: first, the rising up of the head-and-neck unit, as well by dorsi-flexion (dorsally concave) of the cervical column as by dorsi-flexion of the head in relation to the neck, and secondly, an increase of the ventral curvature (ventrally concave) of the anterior thoracic region. The posterior part of the body is stiffly anchored down by its hind limbs. The movement of the head is accompanied by a supplementary shoulder extension of about 25°, which presses the hands against the sand (Fig. 8(c)). The parasagittal components of mm. pectoralis, teres major and triceps and p. scapularis, are, respectively, shortened by 26 %, 23 % and 13 %.

At this final stage of the buttressing phase, the scapula does not show any motion, providing a fixed point for the powerful m. rhomboideus (p. occipitalis and p. cervicalis) which shortens by about 45 %. The m. rhomboideus is presumed to be the main agent for the dorsi-flexion of the head (Fig. 8(c)). It is noticeable that, at this moment, both parts of the muscle possess their greatest arm lever in relation to the occipito-cervical joint (*rh.*, Fig. 10(a)). When the maximum buttressing is reached, the direction of the rhomboideus force vector makes a 90° angle with the resultant of all elbow extensor, shoulder extensor and digit flexor muscles (*Fl.e.*, Fig. 10(b)).

A graphic analysis brings out other peculiarities. A line (*YZ*) drawn parallel to the direction of the animal progression in the sand and passing through the occipito-cervical motion centre (*X*), divides the figure into two 'dynamic areas', since the line *YZ* passes also through the intersection (*W*) of the head dorsi-flexor system and the limb extensor system.

The line that can be drawn from the midlength point of the levers against the sand resistance [upper part of the head (*A*) and lower part of the hand (*B*)] is approximately perpendicular to line *YZ*, and parallel to the action line of the m. trapezius anterior (*t.a.*) between the metacromion and the skull (Fig. 10(b)). Musculus trapezius seems to be the kinetic link between both upper and lower 'jaws' of the pincer-like system compressing the sand. If we consider this system as being in static balance between the soil resistance and the muscular forces, and if we reverse the force directions in both dynamic areas, we see (Fig. 10(c)) that there is a force along the line *YZ* which is directed toward *W*, which means that the sand is submitted to a negative pressure at this level. This is the main point of the whole buttressing phase.

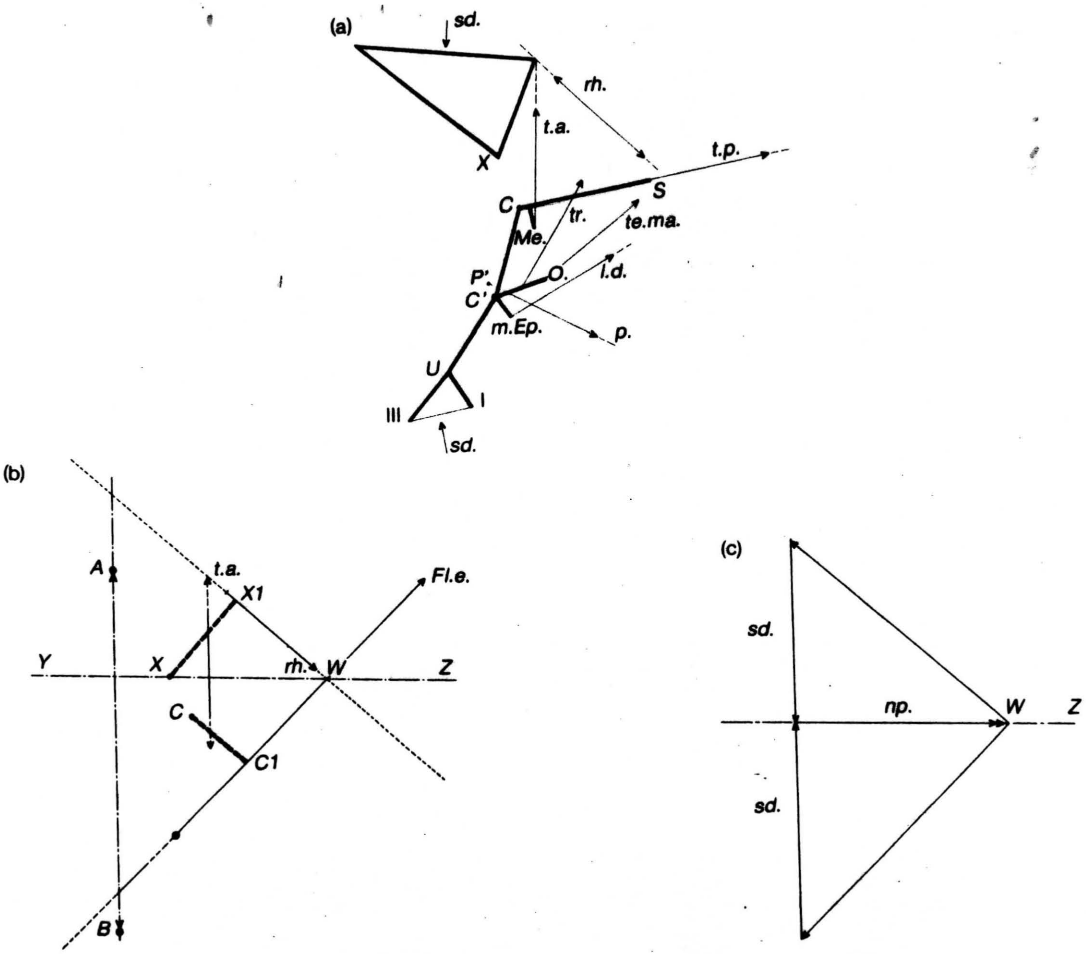


FIG. 10. Diagrammatic representation of the main dynamic peculiarities of buttressing. (a) Lines of action of forelimb muscular forces; (b) main resultant forces of forelimb muscles; (c) theoretical interpretation of the pincer-like system: a negative pressure in front of the animal results from the opening of the superior, i.e. head and neck, and inferior, i.e. forelimbs, jaws of the system. For (a), see legend Fig. 9. "I", axis of the first digit. *A*, point where the head dorsi-flexing force is applied to the upper sand; *B*, point where the forelimb thrust is applied to the lower sand; *C*, scapulo-humeral joint; *C*-C_1, lever arm of $\overrightarrow{Fl.e.}$ in relation to *C*; $\overrightarrow{Fl.e.}$, resultant force of elbow extensor, shoulder extensor and digit flexor muscles; $\overrightarrow{np.}$, negative pressure; $\overrightarrow{rh.}$, rhomboideus; $\overrightarrow{sd.}$, sand resistance; *t.a.*, trapezius, pars anterior; *W*, intersection between the lines of action of the head-dorsi-flexor and forelimb-thrust muscles; *X*, occipito-cervical joint; *X*-X_1, arm lever of the rhomboideus force in relation to *X*; *Y*-*Z*, line through *X* parallel to the direction of the animal progression.

The model that we propose is based upon the hypothesis that the other muscular forces that are involved in the statics of the vertebral column and the hind limbs are neutralized by a static balance in respect of line *YZ*.

We may also notice that, during the buttressing phase, m. latissimus dorsi turns around its lumbar origin, without any length variation. As soon as the forearm is extended, m. dorso-

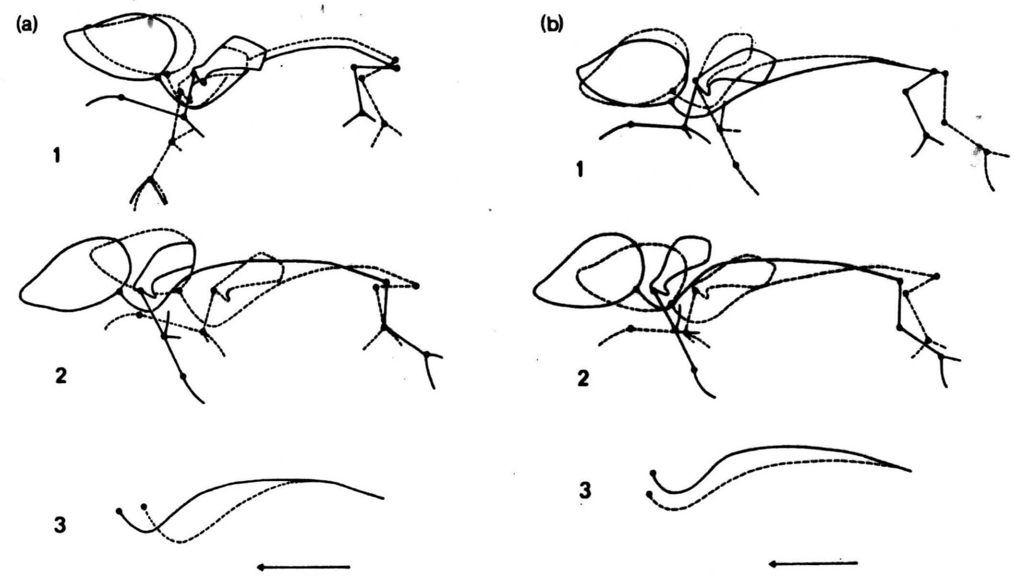


FIG. 11. Diagrammatic representation of the first digging-propulsion phase ((a), 1-3) and the iterative propulsion phase ((b), 1-3), from X-ray cinematography. The movement is pictured from the dashed to the solid outline. (a)$_1$: preparation to digging by a forelimb protraction; (a)$_2$: power stroke; (a)$_3$: variation of the backbone curvature during the power stroke, by superimposing the pelvis of both images of (a)$_2$. (b)$_1$: recovery subphase; (b)$_2$: power stroke; (b)$_3$: variation of the backbone curvature during the power stroke stressed by superimposing the pelvis of both images of (b)$_2$.

epitrochlearis falls in line with latissimus dorsi and the mechanical efficiency of the system for the limb retraction is progressively increased during the whole movement.

Some morphological features make the system of sand compression during the buttressing more efficient: 1) ventral location of the cranio-occipital joint (i.e. maximum arm lever for m. rhomboideus anterior); 2) distal location of the insertions of mm. pectoralis and dorso-epitrochlearis (i.e. increased lever arm for a powerful limb retraction).

Digging-propulsion phase (Figs 11 and 12)

During this phase, the animal achieves its progression in the sand. It also consists of two subphases: 1) a short recovery and 2) a power stroke (backward retraction of the limb) resulting from shoulder and elbow extension. The digging-propulsion phase may be repeated two to five times uninterruptedly after each buttressing phase. The first digging-propulsion following the buttressing is slightly different from the other (Fig. 11(a)) because it starts from the utmost buttressed position with the head strongly dorsi-flexed and the vertebral column arched from a firm anchorage on the hind limbs. A description of the dynamics of the forelimbs, the vertebro-costal axis and the head-and-neck unit during the power stroke of a 'normal' (i.e. first excepted) propulsion phase follows.

The forelimbs

We will consider first the muscular actions upon the pectoral limb and girdle unit when initiating the power stroke from a THEORETICAL point of view (Fig. 12(a)); the system has the following characteristics:

(1) the resultant force ($\vec{n}$.) of the muscles linking the olecranon ($C'O$) to the scapula (SC) should initiate: a) rotation of the forearm $C'U$ (i.e. elbow extension) in relation to the arm CC' (elbow extension); b) backward rotation of the humerus CC' in relation to the scapula CS (shoulder extension), owing to the rotation component $\vec{nr}$. of $\vec{n}$.; c) an upward push of the head of the humerus into the glenoid fossa, owing to the stabilizing component $\vec{ne}$. of $\vec{n}$.

(2) musculus latissimus dorsi (vector $\vec{d}$) acts on the medial epicondyle *m.Ep.* with the following effects: a) backward rotation of the humerus CC' in relation to the scapula SC (shoulder extension) owing to the component $\vec{dr}$. of $\vec{d}$.; b) elevation of the scapulo-humeral joint C, owing to the stabilizing component $\vec{de}$. of $\vec{d}$.

Should we consider now the ACTUAL movement observed at the beginning of the power stroke; it consists of : 1) backward rotation of the humerus by 20° and forward rotation of the scapula by 20° about the fixed scapulo-humeral joint; this means that the elevation components $\vec{ne}$. and $\vec{de}$. are balanced by other forces; 2) the scapula is subjected in its caudal part to forces opposed to the downward rotation components of arm retractors (shoulder extensors and of a greater magnitude; 3) the forces exerted upon the sand by the claws resulting mainly in shoulder and elbow extension.

In order to explain the above contradiction between the theory of muscular action and the movements actually observed, we must consider that other muscular actions play a part in the digging system.

The elevation component for the scapula ($\vec{el}$., Fig. 12(a)) is most likely balanced by lateral and ventral muscles, such as mm. levatores scapulae, dorsalis and ventralis, subclavius and costo-scapularis, which make up a fan widely spread out from the atlas and the third cervical vertebra to the first ribs, and converging on to the scapula. The resultant $\vec{v}$. of these muscles (Fig. 12(b)) is directly opposite to $\vec{el'}$. (component of $\vec{el}$. perpendicular to CS at the beginning of the digging propulsion phase, Fig. 12(a)). Supposing that the line of action of this muscular system is shifted during the movement by successive and out-of-phase firing of the different parts of the muscular fan. If we consider the scapula-arm-forearm system ($CS+CC'+OC'U$), the triceps and teres major tends either to elevate O (when S is fixed), or to lower S (when O is fixed). In the first case, the retraction resultant $\vec{n}$. of the shoulder and elbow extensor muscles (Fig. 12(a)) tends to elevate O. In the second case, the resultant of the same muscular action is a force $\vec{n'}$. equal and opposite to $\vec{n}$. which origins from the intersection *g*. (Fig. 12(b)) of the line of action of $\vec{n}$. with the scapula SC. Since an elevation of S occurs, we may suppose that, as soon as the movement begins, a force $\vec{n''}$., greater than $\vec{n'}$. and opposite to it, is applied in g to SC. The force n''. most likely results in part from the action of m. rhomboideus, p. occipitalis and p. cervicalis, although the torque of their rotation component $\vec{rr}$. (for SC about C) does not reach 0·4 of the magnitude of the equivalent component of the theoretical $\vec{n''}$. The slight stretching of m. trapezius posterior ($\vec{t}$., Fig. 12(b)) could also participate in the elevation of the scapula. But the main factor seems to be found in the couple of forces about C, made up of the resultant $\vec{v}$. of the ventro-lateral muscles (Fig. 12(b)) and the rotation component $\vec{rr}$. of the rhomboideus. Musculus supraspinatus may also take part in the stabilization of the scapula, because its humeral insertion is cranially located in relation to the

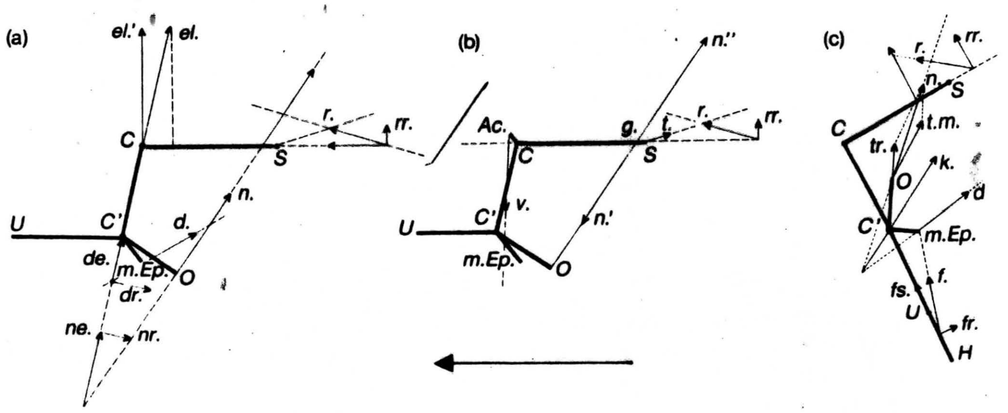


FIG. 12. Theoretical (a) and real (b) arrangements of the lines of action of the forelimb muscular force component during the beginning of the power stroke; and (c) lines of action of forelimb muscle forces at the end of the power stroke (from X-ray cinematography); the direction of the animal progression is indicated by the arrow. Bone lines are mechanical, not anatomical axes (see explanations in the text). *Ac.*, acromion process; *C–C'*, upper arm; *C'–O*, olecranon process; *C'–U*, forearm; $\vec{d}$., latissimus dorsi; $\overrightarrow{de}$., elevation component of $\vec{d}$.; $\overrightarrow{dr}$., rotation component of $\vec{d}$.; *el.*, resultant along *C–C'* of all the arm muscles involved in the shoulder elevation; $\overrightarrow{el'}$., elevation component of $\overrightarrow{el}$., in relation to *S*. (resulting in the dorso-medial rotation of the shoulder blade); $\vec{f}$., resultant of the hand flexor muscles; $\overrightarrow{fr}$., rotation component of $\vec{f}$., $\overrightarrow{fs}$., stabilizing component of $\vec{f}$.; *g.*, intersection of the line of action of the muscular resultant $\vec{n}$ with the scapula *S–C*; $\vec{k}$., resultant of all the muscles acting upon the medial epicondyle and the olecranon process; *m.Ep.*, medial epicondyle; $\vec{n}$., resultant of the elbow extensor muscles; *ne.*, elevation component of $\vec{n}$; $\overrightarrow{nr}$., rotation component of $\vec{n}$.; $\vec{n'}$., resistance of the still scapula to $\vec{n}$. action; $\vec{n''}$., force that is to be applied to *S* in order to counterbalance $\vec{n}$, and to produce the observed rotation of the scapula; *O.*, tip of the olecranon process; $\vec{r}$., resultant of the head dorsiflexor muscles; $\overrightarrow{rr}$., rotation component of $\vec{r}$.; *S–C.*, scapula; $\vec{t}$., trapezius posterior; $\overrightarrow{t.m}$., teres major; $\overrightarrow{tr}$., triceps; *U–H.*, hand; $\vec{v}$., resultant of levatores scapulae, costo-scapularis and subclavius muscles.

gleno-humeral joint. This is a consequence of the permanent medial rotation of the humeral head (Fig. 3(a)) which is kept in that position by the powerful subscapularis system (long lever arm and bulky muscle).

At the end of the power stroke, the dynamic conditions are as follows (Fig. 12(c)): 1) due to the angle between the olecranon axis *C'O* and the axis of the ulnar shaft *C'U*, the force $\vec{n}$. (triceps and teres major) evinces a positive (counterclockwise) torque for a greater magnitude of elbow extension than if the olecranon were in line. This effect is accentuated by the fact that the complete elbow extension is performed at the end of the movement (Fig. 1(b), 8 and 11(b), 2); 2) the torque of $\vec{n}$. becomes negative when the movement ends, i.e. when it would tend to flex the elbow. Since this is contrary to the observed movement, we must assume that the hand flexors $\vec{f}$. and latissimus dorsi $\vec{d}$., inserted on the medial epicondyle, assisted by the dorso-epitrochlearis, inserted on the distal part of the radius, do intervene. The anatomical medial torsion and physiological medial rotation of the humerus set the medial epicondyle in a parasagittal plane, where it forms a long lever arm for the muscles inserted on it. During the whole phase, the digit flexors $\vec{f}$. have a positive torque for this action. The torque is maximum (*C'm.Ep.* at right angles with *C'U*) when the forearm makes an angle of 140° with the arm, at the end of the stroke. At this moment, the digit flexors act as elbow extensors by their component $\overrightarrow{fr}$., the torque of which is important in relationship to the elbow joint *C'*; 3) during the limb retraction, the elevation component of m. latissimus dorsi for the scapulo-humeral joint ($\overrightarrow{de}$., Fig. 12(a)) diminishes progressively and the latissimus dorsi becomes a pure extensor of the shoulder. In Fig. 12(c), where all the parasagittal vectors have the same magnitude, the resultant $\vec{k}$. of m. latissimus dorsi and of mm. triceps + teres major passes close to the elbow joint. This means that at this moment these three muscles are mainly retractors of the limbs. Then, m. dorso-epitrochlearis evidences also its maximum retraction efficiency; 4) during the propulsive action, the rotation component $r\vec{r}$. of m. rhomboideus occipitalis and cervicalis ($\vec{r}$.) increases so that the posterior part of the scapula is raised, which generates a rotation amounting to 20 % of the scapula about the scapulo-humeral joint.

The trunk-and-hind limb unit

The hind limbs change from their static role of anchoring the body to a propulsive action synchronized with the forelimbs. The vertebral column transmits the reaction force by stiffening in its posterior thoracic and lumbar portions (in front and behind the anticlinal hinge area) which become almost rectilinear (Fig. 11(b), 3), supposedly due to epiaxial muscle action. Furthermore, an increased vertebral curvature of the anterior part of the thorax is presumably the result of rectus abdominis contraction, since in the Namib Golden mole, m. rectus abdominis inserts into the cranial end of the manubrium sterni. The synergical contraction of epiaxial and ventral muscular masses may result in the body stiffness necessary to the forward transmission of the soil reaction to the limb thrust.

When the propulsive action ends, the snout has travelled a little farther than the hip joints because of the straightening of the vertebral column. The strides that are immediately performed by each hind limb permit them to secure a new anchorage for the beginning of the next digging-propulsion phase.

The head-and-neck unit

The main resistance from the medium during progression through the sand is applied to the snout. From a biomechanical point of view, the head and cervical column represent the intersection of two sets: the forelimb system and the trunk-hind limb one. The snout tip is lowered a little during progression into the sand, while the dorsally concave curvature of the cervical column decreases. But the path followed by the snout is the result of the combined displacements of different parts of the body against the sand resistance: 1) elevation of the cranial end of the vertebral axis, due to the decrease of the thoraco-lumbar (ventrally concave) curvature; 2) lowering of the same end in relation to the cervico-thoracic hinge, due to the decrease of the cervical (dorsally concave) curvature; and 3) dorsi-flexion of the head about the occipito-cervical joint (Fig. 11). These combined displacements result in the penetration of the head into the sand. Then, the dorsal slope of the head is opposite to the main soil resistance, while the midship frame of the digging system is kept at the level of a line joining the metacromions and the occipital attachments of the trapezius 'hood'. Musculus sterno- and cleido-mastoideus on one hand, trapezius anterior and rhomboideus, p. occipitalis and p. cervicalis, on the other hand, represent the links between the hand-and-neck and forelimb units. The powerful mm. sterno- and cleido-mastoideus are inserted at the back of the occipito-cervical joint because of the ventral location of the foramen magnum and are therefore able to cause the combined movement of ventral flexion of the whole cervical column and head dorsiflexion.

During the propulsive action, the cranial insertion of m. rhomboideus, p. occipitalis and p. cervicalis appears to be the fixed point, while the m. trapezius anterior acts like a hood holding the midship frame area of the whole body (maximum width).

Conclusion

Though *Eremitalpa* is the only truly desert-adapted fossorial insectivore, it does not depart, as far as the musculo-skeletal system is concerned, from other chrysochlorids. Comparing *Eremitalpa* to *Chrysochloris* does not show evidence of significant morphological features that might be ascribed particularly as either phylogenetical or adaptive differences. Rather, the strikingly modified locomotor system of chrysochlorids is well adapted for digging in various types of terrain without further specializations.

The chrysochlorids belong to the group of 'parasagittal head-and-forelimb diggers', as geomyids among rodents, Hill (1937), illustrating one of the numerous mechanisms shown by small mammals to travel under the ground. Others are 'transversal forelimb diggers' (talpids) or 'tooth diggers' (some arvicolids and spalacids, Gasc *et al.*, 1984). These classical categories have to be reconsidered by the analysis of the digging cinematics in live specimens and consequently by the functional understanding of some morphological features.

Besides the chrysochlorids among the parasagittal scratchers, we find few other extant mammals: *Notoryctes*, among marsupials, *Chlamyphorus*, among edentates, despite the lack of detailed experimental analysis of the digging movements of these two genera.

Though the whole body of the Namib Golden mole takes part in the propulsion, the very excavating results from combined parasagittal movements of the shovel-like head, pectoral girdles and forelimbs. For the setting up of such a mechanism, several alterations of the basic mammalian morphological pattern are needed: first, reinforcement of the muscular connections between the head, pectoral girdles and forelimbs, which together make up the 'drilling unit' of the system, and loss of the dorsal muscular links that normally connect the vertebral column with the scapulae; secondly, elongated apophyses, e.g. olecranon and medial epicondyle of the humerus, and distally shifted muscular insertions, e.g. provide longer lever arms for muscular forces, hence greater momentum (the strength of movements is obtained to the detriment of amplitude); thirdly, besides the above-mentioned elongation of muscular lever arms, the shape of the articular surfaces, the medial axial torsion of the humerus shaft, synostoses of several wrist and hand bones and the ossification of the flexor tendon result in the restriction of the degree of freedom of the forelimb within a parasagittal plane, as well as in maintaining the hand in a prone position and increasing the sturdiness of the whole forelimb.

The skeletal features of *Eremitalpa granti namibensis* are also to be found in Oligocene mammals, the Epoicotheres. First described on the basis of skull fragments, the Epoicotheres had been assigned to edentate-like mammals (*Palaeonodonta*) in respect of tooth morphology. The recently discovered post-cranial bones bear a strong resemblance to chrysochlorids down to the smallest details (Rose & Emry, 1983), which suggests two major adaptations characterizing this extinct group: specialized feeding and underground travelling. The sudden extinction of the Epoicotheres constitutes a rather surprising evolutionary problem. In their fine study of the fossils, Rose & Emry (1983) specify that, though several mammalian groups disappeared with the Epoicotheres, other fossorial vertebrates, such as talpids and rhineurids (*Squamata*), have survived until the present. According to these authors, the Epoicothere's disappearance suggests drastic environmental changes, combined with a lack of resistance against competitors. By the example of the Namib Golden mole, we recognize the adaptability of the chrysochlorid locomotor system to sundry kinds of subterranean mediums. Among a wider range of locomotor capabilities, the aptitude for travelling in deep loose sand enables *E. granti namibensis* to find a suitable environment for survival (food supply, temperature, scarcity of predators, etc.), whereas its other capabilities allow for adapting to environmental changes. Such an adaptability hints at the failure of the Epoicotheres to survive resulting more likely from their feeding specialization than digging locomotion.

As opposed to digging in harder soil, where animals can build permanent burrows by excavating soil in mounds as talpids and spalacids do, digging in loose sand evokes swimming, since the falling sand looks like a fluid. Such an analogy cannot be seriously considered since swimming does not imply any modification of the physical property of water, whereas progressing through the sand requires iterative changes of its compactness to decrease the sand resistance in front and to increase it below hands and feet.

The main adaptive feature of digging in deep loose sand is the 'buttressing phase'. Buttressing is related to pressure, since this movement episode is bypassed in locomotor patterns of either superficial foraging burrowing, or initial penetration (see above). The weight of the overlying sand exerts a pressure upon the body of the animal as well as increasing the compactness of the sand. The main function of buttressing, i.e. loosening the sand in front, is not needed when the animal moves close to the surface.

The function of buttressing as a biomechanical response to the physical constraints of the surrounding pressure strengthens Gans' functional analysis of digging movements of *Rhineura* in Amphisbaenia (1960).

Summary

The burrowing locomotion of the Namib Golden mole through deep loose sand was studied by means of the cinefluorographical technique. A buttressing phase is followed by two to five digging-propulsion phases. During the buttressing phase, both forelimbs are fully extended and the powerful claws are anchored downwards in the soil. The head and the anterior part of the body, firmly supported by these struts, dorsiflex, resulting in decompacting the sand in front of the snout by compacting sand above and beneath the trunk. Buttressing is bypassed in shallow sand travelling or in the initial penetration pattern of deep burrowing.

During the digging propulsion phases, the main action results from the simultaneous movements of both forelimbs: a forward protraction of the limb (shoulder flexion + elbow and wrist extension) brings the hands under the chin; followed by a backward power stroke (shoulder extension + elbow and wrist flexion). During the last part of the backward stroke, both hind limbs come into play for propulsing the body by their backwards thrust with the forelimbs.

The detailed anatomical study of bones, ligaments and muscles has been carried out in order to analyse the biomechanics of the locomotor system, to find out the functional significance of some morphological peculiarities (e.g. the third 'flexor' bone and tendon in the forearm) and to discuss the mechanical interaction between muscular forces and soil reaction.

This study would not have been possible without the understanding and authorization of 'the Department of Nature Conservation and Tourism' and the helpful cooperation of the 'Desert Ecological Research Unit' of S.W. Africa-Namibia.

All the credit is due to Pr. Y. Coineau (Muséum national d'Histoire naturelle, Paris) who was the mainspring of the Namib Golden mole odyssey until their arrival in France (Missions 1981 and 1982 to S.W. Africa-Namibia). A. Devèze was responsible for photographs and films taken in the field.

We thank Ph. Doumenc, general manager of UTA French Airlines for transport facilities, and the hostesses for nursing and warming up the hot-water bottle of the animals.

We are especially grateful to F. Letellier for her assistance in giving board and lodging to the animals in the Vivarium of the Muséum national d'Histoire naturelle.

We are greatly indebted to B. Tardieu, ingénieur E.C.A.M., whose knowledge in soil mechanics helped us to elucidate biomechanical problems.

Our gratitude also goes to those colleagues and friends who provided us with fruitful comments, valuable discussions, bibliographical information, and who improved our clumsy English style: M. C. Dane, J. Fleagle, W. P. Luckett, F. Petter and W. D. Haacke, who pioneered researches on Namib Golden moles by catching the first live specimen on the occasion of the official opening of the Namib Desert Research Station (1963).

The 'Service du film de la Recherche Scientifique' (SFRS) participated in the cinefluorographical sequences that are included in the movie *La Namibie, un désert original* (part 2: *Locomotion and thermoregulation*).

We thank P. Mars for producing the illustrations; G. Sanchez, S. Arnold and Joan Kelly for typing the manuscript.

This research has been supported by the Centre national de la Recherche Scientifique (CNRS-ER 246), the Muséum national d'Histoire naturelle (Paris) and the Ministère des Relations extérieures (France).

REFERENCES

Cooper, C. F. (1928). On the ear region of certain of the Chrysochloridae. *Phil. Trans. R. Soc.* **216B:** 265–283.

Dobson, G. E. (1882). *A monograph of the Insectivora, systematic and anatomical.* Part I. London: John van Voorst.

Dobson, G. E. (1892). *A monograph of the Insectivora, systematic and anatomical.* Part II. London: John van Voorst.

Flower, W. H. (1876). *Osteology of the mammalia.* London: Macmillan.

Gans, C. (1960). Studies on Amphisbaenids (Amphisbaenia, Reptilia). 1. A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. *Bull. Am. Mus. nat. Hist.* **119:** 129–204.

Gasc, J. P., Renous, S., Casinos, A., Laville, E. & Bou, J. (1984). Comparison of diverse digging patterns in some small mammals. *Proc. int. Symp. Verteb. Morph.* Fortsch. d. Zool. Stuttgart & New York: Gustav Fischer Verlag.

Govaerts, A. (1962). *La biomecanique. Nouvelle methode d'analyse du mouvement.* Bruxelles: Presses Universitaires.

Hildebrand, M. (1974). *Analysis of vertebrate structure.* New York: John Wiley & Sons.

Hill, J. E. (1937). Morphology of the Pocket gopher mammalian genus *Thomomys. Univ. Calif. Publs Zool.* **42:** 81–171.

Holm, E. (1969). Contribution to the knowledge of the biology of the Namib Desert golden mole *Eremitalpa granti namibensis* Bauer & Niethammer 1959. *Scient. Pap. Namib Desert Res. Stn* No. 41: 37–42.

Jouffroy, F. K. (1971). La musculature des membres des mammifères. In *Traité de Zoologie* **16** (3): 1–475. Grasse, P. P. (Ed.). Paris: Masson.

Jouffroy, F. K. & Gasc, J. P. (1974). A cineradiographical analysis of leaping in an African prosimian (*Galago alleni*). In *Primate locomotion*: 117–142. Jenkins, F. A., Jr. (Ed.). New York & London: Academic Press.

Jullien, R. (1967). Musculature du membre antérieur chez les principaux types d'insectivores. *Mém. Mus. natn. Hist. nat. Paris (Zool.)* **48A:** 1–68.

Kindahl, M. (1949). The embryonic development of the hand and foot of *Eremitalpa* (*Chrysochloris*) *granti* Broom. *Acta zool., Stockh.* **30:** 133–152.

Macalister, A. (1878). *Morphology of vertebrate animals.* London: Longmans Greene.

Meester, J. (1964). Revision of the Chrysochloridae. 1. The desert Golden mole *Eremitalpa* Roberts. *Scient. Pap. Namib Desert Res. Stn* No. 26: 1–18.

Petter, F. (1981). Remarques sur la systématique des chrysochloridés. *Mammalia* **45:** 49–53.

Puttick, G. M. & Jarvis, J. U. M. (1977). The functional anatomy of the neck and forelimbs of the Cape golden male, *Chrysochloris asiatica* (Lipotyphla: Chrysochloridae). *Zoologica afr.* **12:** 445–458.

Reed, C. A. (1951). Locomotion and appendicular anatomy in three soricoid insectivores. *Am. Midl. Nat.* **45:** 513–671.

Roberts, A. (1951). *The mammals of South Africa.* Johannesburg: Trustees of the mammals of South Africa book fund.

Rose, K. D. & Emry, R. J. (1983). Extraordinary fossorial adaptations in the Oligocene palaeonodonts *Epoicotherium* and *Xenocranium* (Mammalia). *J. Morph.* **175:** 33–56.

Roux, G. H. (1947). The cranial development of certain Ethiopian 'Insectivores' and its bearing on the mutual affinities of the group. *Acta zool., Stockh.* **28:** 165–307.

Shortridge, G. C. (1942). Field notes on the first and second expeditions to the Cape Museum's Mammal Survey of the Cape Province: with descriptions of some new subgenera and subspecies. *Ann. S. Afr. Mus.* **36:** 27–100.

Simonetta, A. M. (1956). Alcune osservazioni preliminari sull'orecchio medio e la regione sfenoidale di *Chrysochloris asiatica*. *Atti. Accad. naz. Lincei Rc.* **21:** 134–138.

Simonetta, A. M. (1957*a*). Anatomia e significato morfologico e sistematico dell' orecchio medio e delle strutture ad esso connesse in alcuni insettivori (*Suncus*, *Talpa*, *Chrysochloris*). *Archo ital. Anat. Embriol.* **62:** 55–94.

Simonetta, A. M. (1957*b*). Condrocranio e dermascheletro di *Chrysochloris asiatica* (Linnaeus). *Monitore zool. ital.* **65:** 28–47.

Simonetta, A. M. (1968). A new golden mole from Somalia with an appendix on the taxonomy of the family Chrysochloridae (Mammalia, Insectivora). *Monitore zool. ital.* **2** (Suppl.): 25–55.

Stirling, E. C. (1891). Description of a new genus and species of Marsupialia, *Notoryctes typhlops*. *Trans. R. Soc. S. Aust.* **14:** 154–187.

Walker, E. P., Warnick, F., Hamlet, S. E., Lange, K. I., Davis, M. A., Uible, H. E. & Wright, P. F. (1968). *Mammals of the world* **1.** Baltimore: John Hopkins Press.

Yalden, D. W. (1966). The anatomy of mole locomotion. *J. Zool., Lond.* **149:** 55–64.