Sprawling *versus* parasagittal stance in multituberculate mammals

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The structure of multituberculate humerus and shoulder and elbow joints is analyzed and compared with those of anurans, lacertilians, monotremes, and fossil and extant therian mammals. The following features are recognized as characteristic of the humeri of tetrapods with a primary sprawling stance: prominent radial and ulnar condyles (trochlea in parasagittal forms), lesser tubercle wider than greater tubercle (narrower in parasagittal forms), wide intertubercular groove (narrow in parasagittal forms). Torsion of the humerus occurs in terrestrial tetrapods with abducted forelimbs, which use symmetrical diagonal gaits, but not in anurans which have abducted forelimbs but use asymmetrical jumps, and not in fossorial therians with sprawling or semi-sprawling stance (except Chrysochloridae). Lack of torsion is not indicative of parasagittalism. Condylar structure of the elbow joint, characteristic of multituberculates, occurs in all tetrapods with primary abducted forelimbs. Fossorial therians that secondarily acquired half-sprawling or sprawling stance, differ from tetrapods with primary sprawling stance in having a trochlea and radial condyle, but no ulnar condyle, and in having a narrow intertubercular groove. The hypotheses of Sereno & McKenna on multituberculate parasagittal stance and of Kielan-Jaworowska & Gambaryan on sprawling stance are tested by anatomical comparisons and reconstructions of forelimb movements. It is shown that the range of humeral excursion during flexion-extension at the shoulder joint in multituberculates was much smaller than in *Didelphis*, and that during the swing phase the forelimbs were stretched anteroventrally, as characteristic of mammals before landing. It is concluded that multituberculates were adapted for asymmetrical jumps with abducted forelimbs, rather than that they moved like *Didelphis*. As there is no trace of an incipient trochlea in any known multituberculate, while the trochlea made its appearance in therians possibly during the Late Jurassic, the idea that parasagittalism occurred in mammalian evolution in common ancestors of therians and multituberculates is refuted.

Key words: Multituberculata, Theria, anatomy, digging, sprawling stance, parasagittalism.

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Introduction

Extant therian mammals (marsupials and placentals) differ from monotremes, among other ways, in limb posture, which is abducted in monotremes and more or less parasagittal in therians. Among the therians, due to adaptations to the fossorial mode of life, the Talpidae secondarily acquired abducted position of the forelimbs, while Chrysochloridae, Myospalacidae and, apparently, extinct Palaeanodonta abduct (abducted) their limbs during digging.

Conclusions on the gait of extinct vertebrates should be based on osteology and ichnology. In the case of Mesozoic mammals, however, trackways have been found only in a single Late Jurassic locality in Argentina (Leonardi 1994 and references therein) and it is not known to which mammalian group these tracks belong. Another difficulty in reconstructions of the gait of Mesozoic mammals concerns the scarcity of the postcranial elements and their small size (see Lillegraven *et al.* 1979 and references therein; Jenkins & Schaff 1988; Kielan-Jaworowska 1989; Krebs 1991; Krusat 1991; Kielan-Jaworowska & Gambaryan 1994; Sereno & McKenna 1995; Li *et al.* 1995; Dashzeveg *et al.* 1995).

The question arises whether multituberculates retained a sprawling stance throughout their history, or acquired a parasagittal stance. In the latter case, did the common ancestor of therians and multituberculates acquire a parasagittal posture, as argued by Sereno & McKenna (1995), or did therians and multituberculates independently acquire parasagittal postures? The answer to this question has an important bearing on the phylogenetic position of multituberculates.

Sereno & McKenna (1995) published a preliminary description of a complete shoulder girdle, associated with the proximal segments of the forelimb of the Late Cretaceous multituberculate from Mongolia (cf. *Bulganbaatar nemegtbaataroides*, referred to further as *Bulganbaatar*), and demonstrated a small (approx. 15°) degree of torsion of the humerus. They argued that the multituberculate forelimb stance was similar to that in therians (parasagittal) rather than abducted, as reconstructed by Kielan-Jaworowska & Gambaryan (1994).

If the conclusions of Sereno & McKenna (1995) on parasagittalism of multituberculate limbs are valid, this would support the hypothesis on the sister group relationships of Multituberculata and Theria (promoted also e.g., by Rowe 1988; Lucas & Luo 1993; McKenna 1996; Stidham 1996). The validity of such a conclusion requires, however, that this postural style of the forelimbs should occur in all the multituberculates, or at least in basal multituberculates.

The Late Triassic–Early Jurassic Haramiyidae possibly are not related to multituberculates (Jenkins *et al.* 1996). The oldest uncontested multituberculates derive from the Late Jurassic of Portugal (Hahn 1969, 1993 and references therein). All older purported multituberculates – *Mojo* from the Liassic of Belgium (Hahn *et al.* 1987), and unnamed fragments from the Bathonian of England (Freeman 1979 and references therein, see also Kermack 1988) – are represented by broken teeth. The multituberculate nature of these fragments is possible, but cannot be unequivocally demonstrated. The Kimmeridgian multituberculates from Portugal are represented by numerous broken skulls, lower jaws and isolated teeth (Hahn 1993 and references therein), but their postcranial fragments have not been described. In the collection of Purbeck (latest

Jurassic or earliest Cretaceous) from England (Simpson 1928a; Kielan-Jaworowska & Ensom 1992) postcranial fragments have not been encountered either. The same concerns multituberculates from the Morrison Formation of North America (Simpson 1929).

In the collection of Early Cretaceous multituberculates from the Aptian or Albian of Khoboor in Mongolia (Kielan-Jaworowska *et al.* 1987), housed in the Paleontological Institute in Moscow, there are some purported multituberculate postcranial fragments, which have not been described. Kielan-Jaworowska & Nessov (1992) described a proximal fragment of a humerus and a proximal fragment of a femur from the Coniacian of Uzbekistan. The multituberculate materials from the Late Cretaceous of Mongolia contain several incomplete postcranial skeletons (Simpson 1928b; McKenna 1961; Kielan-Jaworowska & Dashzeveg 1978; Kielan-Jaworowska 1989; Kielan-Jaworowska & Gambaryan 1994; Sereno & McKenna 1995). The majority of the Late Cretaceous and Paleocene materials from North America contains only postcranial fragments (Deischl 1964; Sahni 1972; Krause & Jenkins 1983).

The most complete multituberculate shoulder girdle and forelimbs are those of the Late Cretaceous *Bulganbaatar* (Sereno & McKenna 1995). Prior to this finding, Kielan-Jaworowska & Qi (1990) described two complete multituberculate humeri of Eocene *?Lambdopsalis bulla* from China (referred to further as *Lambdopsalis*). On this basis, as well as on an analysis of several multituberculate postcranial fragments from Asia and North America, including especially well preserved pelvic girdle and hind limbs, Kielan-Jaworowska & Gambaryan (1994: fig. 61) reconstructed the multituberculate posture as sprawling.

In order to test the opposing conclusions of Kielan-Jaworowska & Gambaryan (1994) on one side, and of Sereno & McKenna (1995) on the other, concerning the posture of multituberculate forelimbs, we shall analyze the suite of characters that distinguish the shoulder joint, humerus, and elbow joint that differ in a sprawling stance (in tetrapods that use either symmetrical or asymmetrical gaits) from those in a parasagittal stance. As *Lambdopsalis* from China was probably semi-fossorial in its habits, among the therians studied for comparison we include also fossorial forms.

Institutional abbreviations: AMNH – American Museum of Natural History, New York; IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; PSS-MAE – Paleontological and Stratigraphical Section (PSS) of the Geological Institute, Mongolian Academy of Sciences, Ulan Bator, and collections of the joint Mongolian Academy of Sciences-American Museum of Natural History Paleontological Expeditions (MAE); ZIN – Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warsaw; ZPAL UW – Institute of Geology, University of Warsaw.

Other abbreviations: m. – muscle; mm. – muscles.

Terminology and methods

We refer to the posture of limbs of therian mammals as parasagittal. In many therian mammals, however, the humeri function at angles 10–30° from the parasagittal plane, while the femoral axes are positioned 20–50° from the parasagittal plane (Jenkins 1971a, 1974; Jenkins & Weijs 1979). As the shoulder and hip joints are closer to the sagittal plane than the maximum width of the trunk, the humerus and

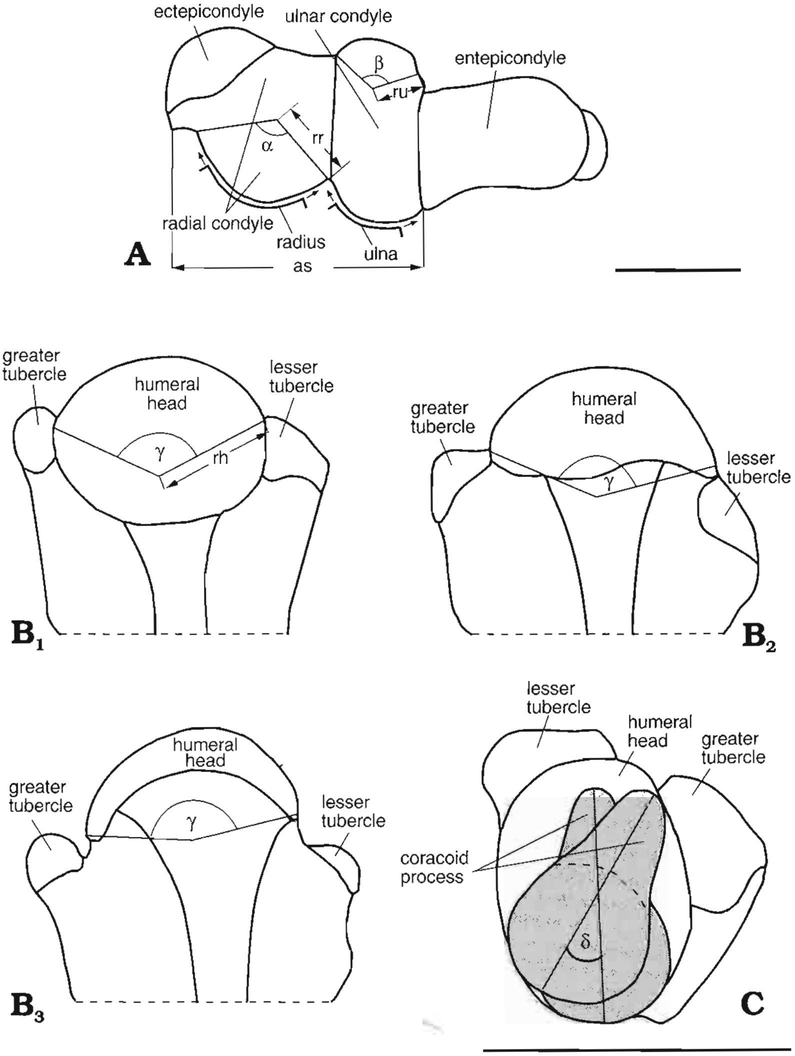


Fig. 1. Diagrammatical drawings showing the method of measurements. **A**, **B**. Left humerus of *Lambdopsalis*. **A**. Distal view (dorsal is up), showing the excursion (arrows) of radius and ulna about the condyles. **B**. Proximal epiphysis. $\mathbf{B_1}$ – dorsal view (horizontal position), $\mathbf{B_2}$ – oblique view with distal epiphysis elevated dorsally 45°, $\mathbf{B_3}$ – oblique (almost vertical) view with distal epiphysis elevated for 85°. **C**. *Nemegtbaatar*, proximal view of the right humerus and outline of glenoid fossa of the scapula (hatched areas) superimposed on the humeral head, in two extreme positions. α, β, – angles of convexities: α – of the radial condyle, β – of the ulnar condyle (position a in Table 1), γ – of the humeral head; δ – angle of rotation of the glenoid fossa about the humeral head; as – width of the whole articular surface of the distal epiphysis; rh, rr, ru – lengths of the radii: rh – of the humeral head, rr – of the radial condyle, ru – of the ulnar condyle. Scale bars are 5 mm, the upper scale is for **A** and **B**, the lower for **C**.

femur abduct at the beginning of the propulsive phase to avoid contact with the trunk. The antebrachium and crus are directed obliquely with respect to the sagittal plane. Therefore the manus and foot are situated closer to the sagittal plane than the elbow and knee joints.

Thus the main difference between the abducted (sprawling) and parasagittal limbs does not concern the angle of humeral and femoral abduction from the sagittal plane, but the positions of hands and feet during the propulsive phase in respect to this plane. In tetrapods with sprawling posture the hands and feet are situated far away from the sagittal plane, while in tetrapods with parasagittal posture they are positioned close to this plane. Another important difference concerns the plane in which the ulna moves. While in the sprawling posture the ulna moves in three planes perpendicular to one another, in parasagittal posture, the presence of a humeral trochlea restricts movement to one plane, which is perpendicular to the transverse axis of the elbow joint.

For defining the convexity of the condyles quantitatively (Fig. 1A), we placed the humerus vertically on the humeral head under a binocular microscope (position 0° in Table 1 and Fig. 2), and made a drawing of its distal extremity with camera lucida. On this drawing we measured the angle of the convexities of both condyles (angles in Fig. 1A, and columns a in Table 1) and the ratio of the radius of each condyle to the width of the whole articular surface (rr/as and ru/as in percent in Fig. 1A and columns b in Table 1). Then we turned the distal end of the humerus 30° upwards (position 30° in Fig. 2), made a drawing of the distal end and repeated the measurements. We continued to turn the humerus in 30° increments until position 120° (Fig. 2). As the data obtained for positions 30° and 60° were very close to one another, we omitted position 30° in Table 1. The last columns in Table 1 give the mean angle of the convexity (including position 30°) and mean ratio of lengths in columns b.

In order to measure the convexity of the humeral head, we placed the humerus under the binocular microscope in dorsal view, in a horizontal position (position 0°) and drew the contour of the head with camera lucida (Fig. 1B). On the drawing we found the radius of the arc of the convexity and measured its angle. Then we elevated the distal part of the humerus dorsally by 45° and then up to 85°, and made drawings and measured the angles again. It proved impossible to make the drawing at the position of 90° (vertical), as then the distal epiphysis obscured the contour of the head.

We are aware that the shapes of the humeral condyles and heads sometimes do not correspond to a sector of a circle, but rather of an ellipse. Therefore our measurements of the angles of the arcs of the condyles (Table 1) and humeral heads (text) are not always precise. Still, they better describe the convexity of these structures than the subjective statements such as ‘convex’ or ‘flat’.

In order to measure the amplitude of flexion-extension of the humerus in the shoulder joint, we placed the humerus on a needle, held in plasticine, under the binocular microscope. The scapula was also placed on the needle and held in plasticine. Under the binocular microscope we moved the glenoid fossa about the humeral head and measured the angle of amplitude. The result was tested on camera lucida drawings of the humeral head and glenoid fossa in various positions (Fig. 1C). On the drawings we also measured the possible angle (δ) of rotation of the glenoid fossa in respect to the humeral head, using contours of the humeral head drawn in proximal view and mirror images of the glenoid fossa in distal view.

Structure and function of forelimbs in some extant and fossil terrestrial tetrapods

The majority of extant tetrapods with sprawling stance (Urodela, Lacertilia, Crocodylia, and Monotremata) use symmetrical diagonal gaits (Gambaryan 1967, 1974; Sukhanov 1974), referred to also as lateral sequence gaits (Hildebrand 1988), in which

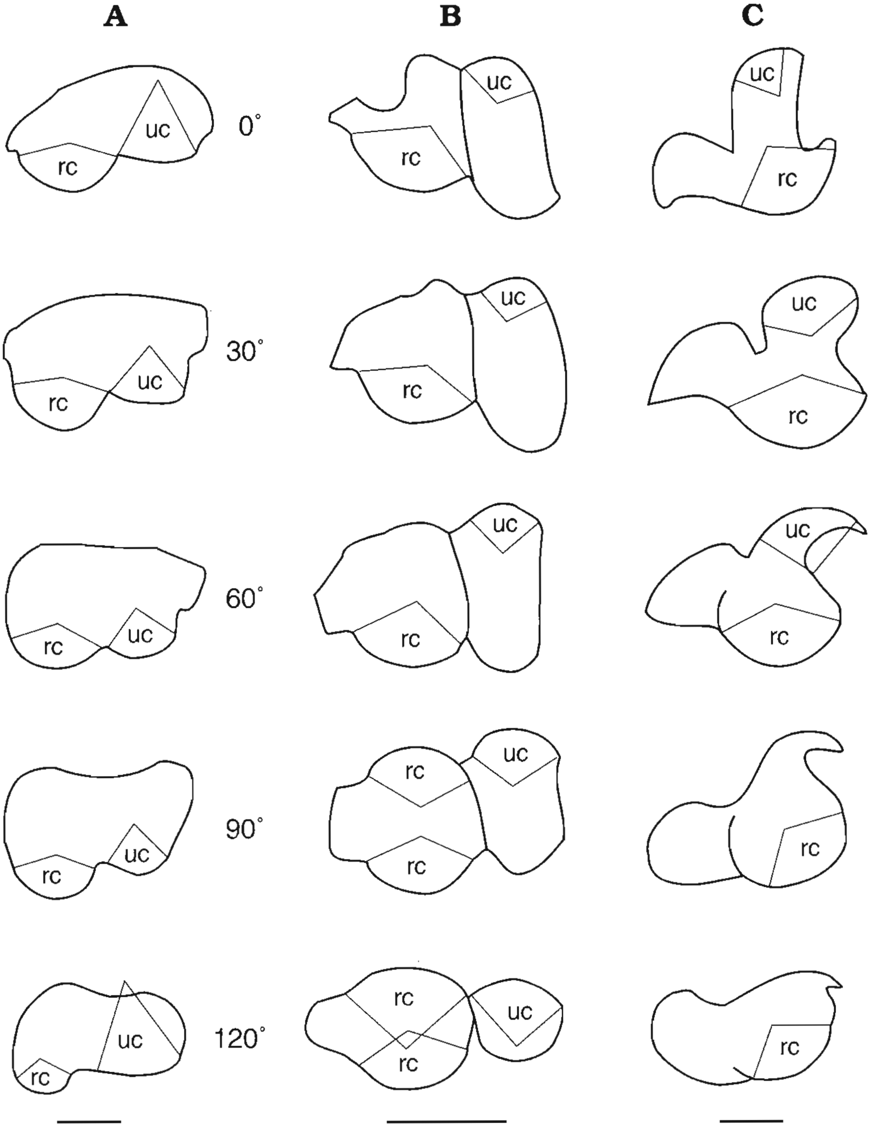
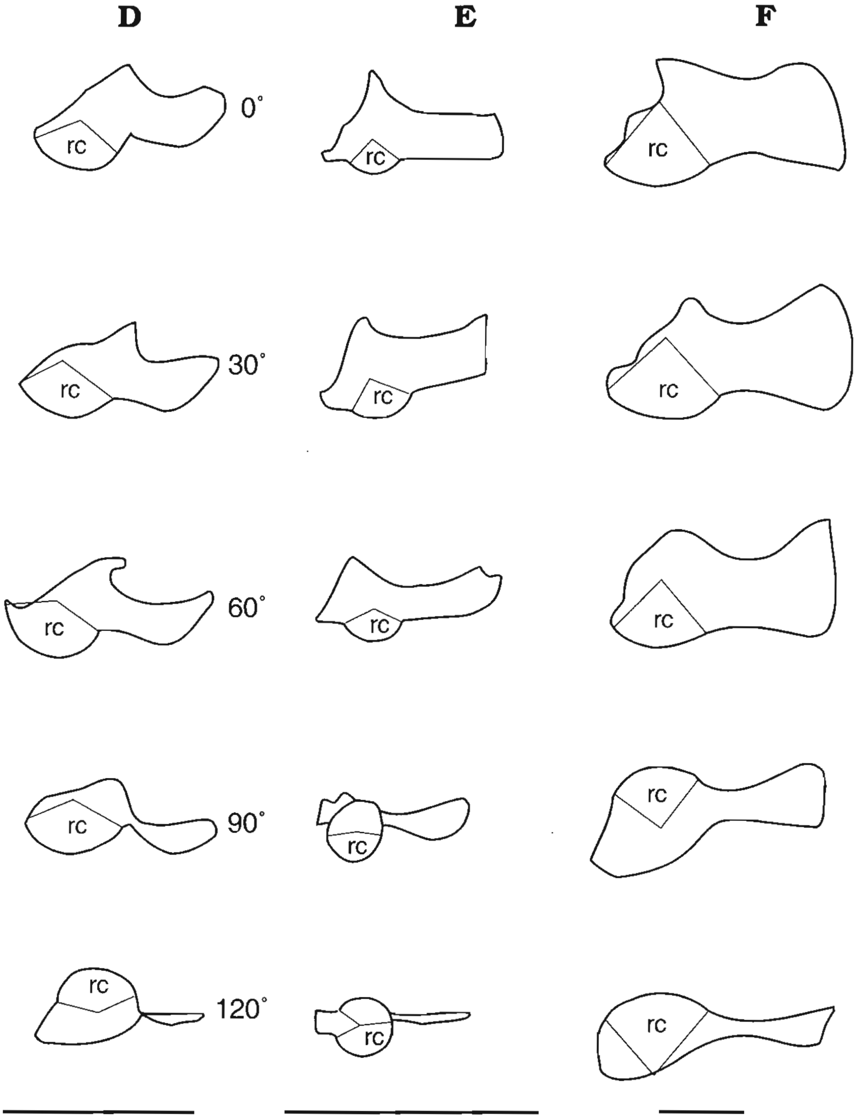


Fig. 2. Camera lucida drawings of the articular surfaces of the humeri, showing angles of the convexities of the condyles, measured at distal view of left humeri (epicondyles omitted), placed on the humeral head. Dorsal is up. 0° vertical position of the humerus, 30–120° – positions of humerus rotated dorsally with →

movement of one forelimb is followed by movement of the opposite hind limb, after which the next forelimb and next hind limb move; at the same time lateral flexures of the body take place (Schaeffer 1941). The only groups of extant tetrapods that have sprawling stance and use asymmetrical gaits (in which the forelimbs move first and then the hind limbs) are the Anura and the Crocodylia (only when running fast). As an example of sprawling stance with asymmetrical gaits we shall discuss Anura; as



respect to the vertical position, for angles shown on the figure. **A**. *Varanus*. **B**. *Lambdopsalis*. **C**. *Tachyglossus*. **D**. *Talpa*. **E**. *Chrysochloris*. **F**. *Myospalax*. Note that in *Varanus* the condyles do not extend onto the dorsal side. The ulnar condyle, characteristic of *Varanus*, *Lambdopsalis* and *Tachyglossus*, does not occur in Theria (**D**–**F**). Scale bar are 5 mm.

Table 1. Convexity of the radial and ulnar condyles along the articular surface seen at four different angles

Species and condyles		0°		60°		90°		120°		Mean	
		a	b	a	b	a	b	a	b	a	b
Varanus griseus ZIN 508	rc	150	25	138	24	138	22	110	20	135	23
	uc	58	42	90	25	85	23	55	50	75	33
Tach. aculeatus ZIN 31024	rc	120	31	138	30	120	30	118	26	127	29
	uc	75	23	99	30	–	–	–	–	91	26
Orn. anatinus ZPAL Mw/2	rc	108	43	110	59	105	55	108	46	108	52
	uc	120	17	170	19	105	17	-	-	141	17
Lambdopsalis bulla IVVP V8408	rc	125	30	115	30	135	27	128	29	125	29
	uc	112	20	110	20	108	24	93	24	106	22
Lambdopsalis bulla IVVP V9051	rc	120	29	117	30	125	30	120	30	120	30
	uc	116	29	113	24	105	24	100	22	108	25
Krypt. saichanensis PSS 8-2	rc	150	20	111	28	140	21	138	21	130	24
	uc	118	17	113	20	120	20	120	20	118	19
Trich. vulpecula ZIN 31713	rc	79	36	85	30	78	26	80	33	81	31
Echinosorex sp. ZIN n.n.	rc	46	45	40	70	30	18	–	–	39	51
Neurotrichus sp. ZIN n.n.	rc	114	28	81	27	72	30	120	21	94	26
Talpa europaea ZIN n.n.	rc	120	25	142	28	120	28	125	21	130	26
Chrysochloris aureus ZIN n.n.	rc	108	18	120	13	168	13	173	13	138	14
Nannospalax nehringi ZIN 219	rc	50	45	40	45	40	40	30	40	40	44
Myospalax myospalax ZIN 386	rc	83	34	70	24	80	44	96	34	82	34

Abbreviations: a – angle of the arc of condyle, (0°) – measured at the vertical position of the humerus, distal view of the condyles, (60°, 90°, 120°) – measured at angles of the humerus, rotated dorsally in respect to the vertical position, so that the condyli are seen only in ventral view; b – ratio of the length of radius of condyle arc to maximum width of the whole articular surface, in percentages (see Figs 1 and 2 for explanation); *Krypt.* – *Kryptobaatar*, n.n. – no number; *Orn.* – *Ornithorhynchus*; rc – radial condyle; *Tach.* – *Tachyglossus*; *Trich.* – *Trichosurus*; uc – ulnar condyle; Mean – mean values of a and b, including also data of the position of 30° (see Fig. 2), not included into the Table.

examples of sprawling stances with symmetrical gaits – the Lacertilia and Monotremata; as examples of non-fossorial mammals with parasagittal posture – some primitive Theria; finally fossorial Theria which acquired a sprawling or half-sprawling stance.

Our analysis of the structure and movements of the forelimbs in extant tetrapods is simplified, because we discuss only the characters that distinguish the sprawling and parasagittal patterns.

Anura. — Comparison of the structure of anurans with that of other tetrapods poses difficulties because of the high specialization of the anurans. The coracoid and scapula (sometimes also the clavicle) contribute to the glenoid fossa, which is concave (not saddle-shaped, as in lacertilians and monotremes, see below) and faces more ventrally than laterally. The humeral head is spherical and there is no torsion. As the bones of the antebrachium are fused, on the distal end of the humerus there is a very large spherical radial condyle (eminentia capitata) which articulates with the fused radius and ulna, while the ulnar condyle is vestigial and does not contribute to the joint (Thireau & Marolle 1968; Minkoff 1975).

The mechanics of jumping in Anura has been investigated by, among others, Gans (1961), Gray (1968), and Emerson (1983). In anurans the trajectory of jump is very steep, the angles of take off and landing are each 35–40° (Gray 1968: fig. 6.12). Before landing, the frog extends the forelimbs anteroventrally, so that the humeri are close to the parasagittal position. The manus is placed in prolongation of the antebrachium, both at 80° to the horizontal. At landing the humerus strongly abducts acquiring a transverse position, the elbow joint flexes and the humeral head is situated lower than the elbow joint. In shoulder joint there occur medial rotation, flexion-extension and abduction-adduction; in elbow joint pronation, flexion-extension and abduction-adduction. These movements are possible because of the spherical structure of the humeral head and distal condyle. Because of the anteroventral direction of the forelimbs at the beginning of landing, the glenoid fossa faces lateroventrally rather than laterally.

Lacertilia (e.g., *Polydaedalus niloticus* and *Varanus griseus*) (Figs 2A, 3A, 7A, 8A). — In *Varanus*, both scapula and coracoid contribute to the glenoid fossa, the coracoid part being wider than the scapular. The glenoid has a saddle-shape surface with a convex medial part and faces posterolaterally.

In *Varanus* and *Polydaedalus* both proximal and distal epiphyses of the humerus are strongly expanded; the torsion is 60°. The articular surface of the head is transversely elongated and faces almost proximally. The head is asymmetrical; its medial side is reflected ventrally, the middle part dorsally, while the lateral part is narrow and directed transversely (Fig. 8A). The middle part of the head overhangs the shaft dorsally (Fig. 8A$_2$). The transverse diameter of the lesser tubercle is larger than that of the greater tubercle, which is poorly defined. Extending from the lateral end of the greater tubercle there is a prominent crest of the tubercle, strongly bent ventrally (Fig. 3A). The poorly defined intertubercular groove occupies about 60% of the width of the proximal epiphysis. While in lacertilians several muscles pass along the intertubercular groove, in therians there is only a tendon. The distal end of the humerus is divided by the intercondylar groove into radial and ulnar condyles. The radial condyle is 35% longer than the ulnar one, compressed laterally and its convexity is greater than that of the ulnar condyle, as shown in Table 1 and Fig. 2A. The surface of the longitudinal axis of the radial condyle is at 25° to the longitudinal axis of the shaft, while the longitudinal axis of the ulnar condyle is parallel to the axis of the shaft (Fig. 3A).

The articulation for the radial condyle on the head of the radius, in proximal view, is dorsoventrally elongated and concave. The length of its arc is smaller in both anteroposterior and transverse directions than the corresponding arcs of the radial condyle. The articular surface for the ulnar condyle on the ulna is concave and consists of two surfaces at about 80° to one another. Flat, triangular surfaces on both radius and ulna form an articulation between the two bones; the articular surface on the ulna is wider than that on the radius. In lacertilians the ulnar and radial condyles are seen only in ventral and distal view, and do not extend onto the dorsal surface (Fig. 7A). This is consistent with the horizontal orientation of the humerus during the whole propulsive phase. As the extension at the elbow joint is small, the condyles would be useless on the dorsal side.

As demonstrated by Jenkins & Goslow (1983), in *Varanus exanthematicus* at the beginning of the propulsive phase the elbow joint is extended to 110–125°. During the first half of the propulsive phase, the elbow joint is flexed to an angle slightly less than 90°. By the end, the elbow joint extends again to an angle between 120 and 135°. By the end of propulsion, the humerus is retracted to form an angle of between 120 and 135° with the median plane and rotated medially by 30–40°. An analysis of the convexity of the radial and ulnar condyles (Table 1 and Fig. 2) allows to establish in which stage of the propulsive phase the mobility of the elbow joint (abduction-adduction and rotation) was the greatest. The angles from 0 to 120°, at which the humerus has been drawn, show the most extended (at 0°) and the most flexed (at 120°) positions of the elbow joint, in all studied tetrapods. In *Varanus* the greatest mobility is at the beginning and at the end of propulsion.

An active rotation of the humerus during the propulsive phase increases the transverse diameter (perpendicular to the length of the humerus) of the lesser tubercle (Figs 3A, 8A). This is due to the

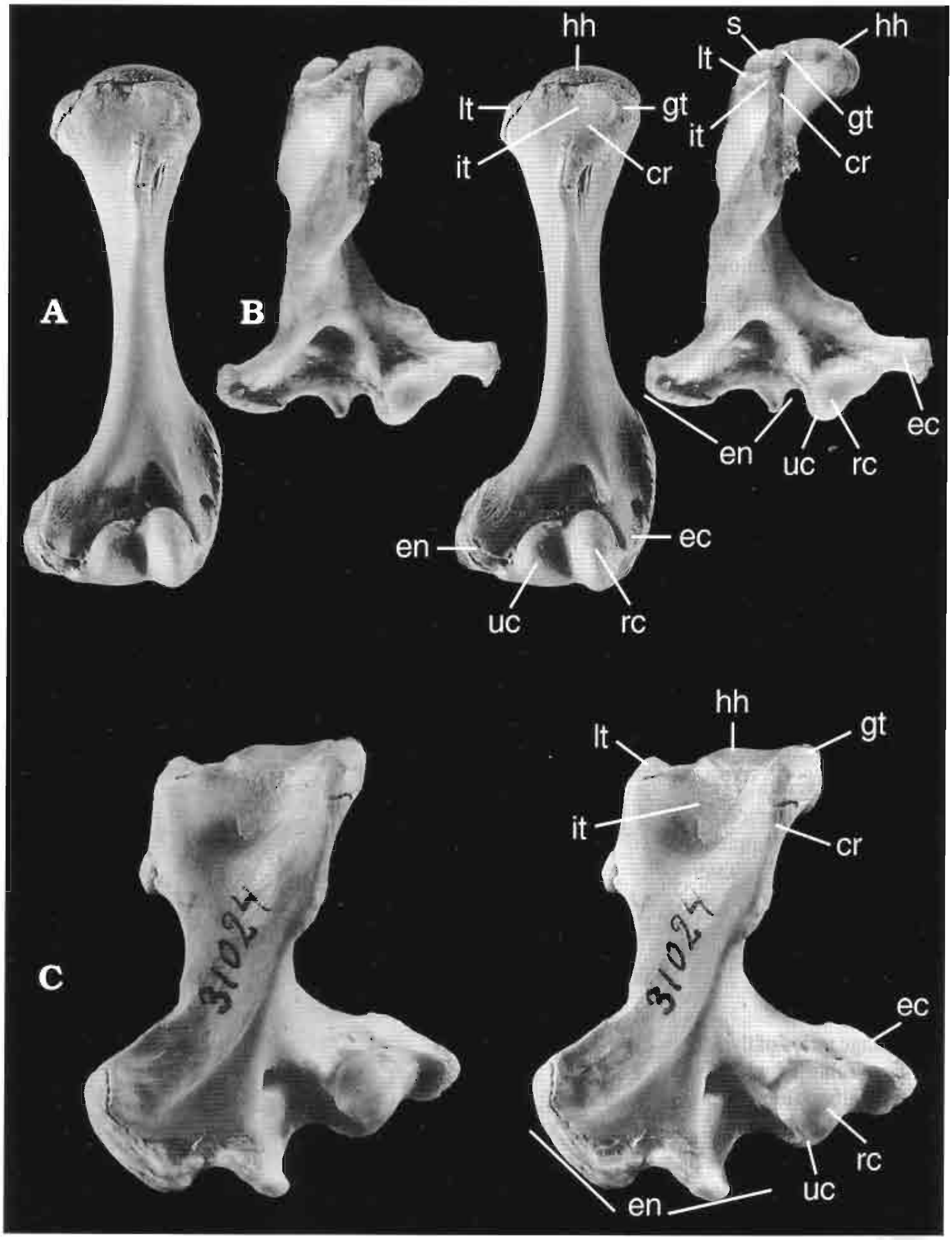


Fig. 3. Stereo-photographs of left humeri in ventral view, Recent. **A**. *Polydaedalus niloticus* (Varanidae), ZPAL UW E-10d, × 1. **B**. *Ornithorhynchus anatinus*, ZPAL Mw-2, × 1.5. **C**. *Tachyglossus aculeatus*, ZIN 31024, × 1. cr – crest of the greater tubercle, ec – ectepicondyle, en – entepicondyle, gt – greater tubercle, hh – humeral head, it – intertubercular groove, lt – lesser tubercle, rc – radial condyle, s – sesamoid bone, uc – ulnar condyle.

insertion on the lesser tubercle of mm. subscapularis and scapulohumeralis posterior, which are responsible for the rotation. An increase of the transverse diameter of this tubercle results in an increase of the moment arm of these muscles. On the crest of the greater tubercle, which is bent ventrally, m. pectoralis inserts, which is also responsible for the rotation of the humerus.

Because of the medial rotation of the humerus during the propulsive phase, the ectepicondyle which at the beginning of this phase is situated medially to the entepicondyle, at the end of the phase is placed laterally to the entepicondyle. The radial condyle traces a longer trajectory than the ulnar condyle, and the trajectory of the proximal part of the radius is longer than the trajectory of the ulna. This is caused by the longer proximo-distal axis of the radial condyle than that of the ulnar condyle and its position at angle of 25° to the longitudinal axis of the humerus. The articular surface for the ulnar condyle on the ulna allows abduction-adduction and flexion-extension, but prevents rotation movements. In addition, the radio-ulnar articulation allows for distal excursion of the radius in relation to the ulna. Because of a transverse displacement of the flat articular circumference (circumferentia articularis Davies & Davies 1962; Schaller 1992) across the radial notch on the ulna, the radius and ulna cross one another. The length of the arc of the concavity of the radial head is smaller in both anteroposterior and transverse directions than the corresponding arcs of the radial condyle, and the following movements: extension-flexion, abduction-adduction and small rotation of the radius occur in this articulation.

Monotremata (Figs 2C, 3B, C, 7C, D, 8E, F). — In monotremes (as in lacertilians) the scapula and coracoid contribute to the glenoid fossa, the coracoid part being wider than the scapular. The glenoid fossa has a saddle-shape surface with a convex anterior part and faces laterally.

In monotremes the proximal and in particular the distal epiphyses of the humerus are strongly expanded; the torsion is 45–60° in *Tachyglossus*, and 70–85° in *Ornithorhynchus* (personal measurements and Simpson 1928a). The head is symmetrical; its articular surface faces proximally, and the middle of the head overhangs the shaft dorsally. When seen in proximal view the head is concave in the middle, the concavity being deeper in *Ornithorhynchus* than in *Tachyglossus* (Fig. 8E$_1$, F$_1$). The lesser tubercle is placed further away from the middle of the humeral head than the greater tubercle; this increases the moment arm of m. subscapularis and m. proscapulohumeralis which insert on the lesser tubercle. The crest of the greater tubercle, on the medial side of which inserts m. pectoralis, is strongly bent ventrally. The intertubercular groove is poorly defined and extends for 50% of the width of the proximal epiphysis in *Ornithorhynchus* and 60% in *Tachyglossus*. Mm. biceps brachii, coracobrachialis, supracoracoideus and part of pectoralis pass along the groove, in contrast to therians (see below) where the intertubercular groove houses only the tendon of m. biceps brachii. In the distal epiphysis, radial and ulnar condyles are conjoined (Jenkins 1973), the radial part being seen on the ventral side and partly in distal view, the ulnar in dorsal and distal views. The entepicondyle is enormous, extending for about a half of the epiphysis width; the ectepicondyle is shorter, but still projects strongly laterally, especially in *Ornithorhynchus*. The radial condyle in *Tachyglossus* is spherical and in *Ornithorhynchus* elongated transversely (Fig. 3B, C). This results in different percentage ratios of the lengths of the radius of condylar arc to maximum width of the whole articular surface (Table 1), which is 29 in *Tachyglossus* and 52 in *Ornithorhynchus*.

The elbow joint is of the ball-and-socket type, with a spoon-shaped, longitudinally elongated surface on the ulna and an oval concavity on the proximal part of the radius, arranged perpendicularly to the spoon-shaped surface on the ulna. Both these surfaces move about the conjoined radio-ulnar condyle. There is also a flat, triangular surface on the ulna that articulates with the roughly rectangular surface on the head of the radius. The transverse diameters of these surfaces are almost equal to each other and therefore the movement between these bones is limited.

The functional analysis of the monotreme forearm has been done by, among others, Haines (1946), Jenkins (1970, 1973) and Pridmore (1985). In *Tachyglossus*, during the propulsive phase the longitudinal axis of the humerus remains roughly perpendicular to the sagittal plane. Because of the strong torsion of the humerus, during the middle of the propulsive phase, the humeral head is situated lower than the elbow joint, and in order to retain the horizontal position of the humerus, the head overhangs the shaft dorsally. Propulsion takes place mostly due to the medial rotation in the shoulder joint. At the same time the elbow joint flexes and the antebrachium rotates medially for about 55°. Radius and ulna move together in different directions about the spherical, conjoined radio-ulnar condyle. The flat radio-ulnar articulation allows a small displacement of the radius relative to the ulna, but not rotation. Some pronation and supination is possible by conjoint movement of the radius and ulna on the radio-ulnar condyle (Jenkins 1973), but independent pronation-supination is impossible because articular circumference and radial notch are of the same size, and the radius and ulna are bound together by an interosseous ligament (Haines 1946).

In *Ornithorhynchus*, the rotation of the humerus occurs as in *Tachyglossus*, the difference, however, is that in *Ornithorhynchus* the humerus retracts by 40°, the head elevates and there is extension in the elbow joint rather than flexion. The larger excursion of movements in the shoulder joint results in differences in structure of the humeral head, which in *Ornithorhynchus* overhangs the shaft more strongly dorsally than in *Tachyglossus.*

Non-fossorial Theria (e.g., *Barunlestes*, *Trichosurus*, and *Cercopithecus*) (Figs 4, 8J). — In therians only the scapula contributes to the glenoid fossa, which is concave, ellipsoidal or rounded. The therian shoulder and elbow joints were discussed by, among others, Jenkins (1971a, 1973 and 1974), and Jenkins & Weijs (1979).

The proximal and distal epiphyses of the humerus in most therians are only little or not expanded and almost parallel to one another; there is only very little or no torsion. The articular surface of the head faces more dorsally than proximally. In most Theria the lesser tubercle is distinctly smaller than the greater tubercle, on which the main extensors of the shoulder joint, mm. supraspinatus and infraspinatus insert. The intertubercular groove is narrow, ranging between 14–23% of the proximal epiphysis width (Kielan-Jaworowska & Gambaryan 1994). Only the tendon of m. biceps brachii passes along the intertubercular groove.

In' most therians a broad concave surface – the trochlea – replaces the ulnar and radial condyles, which as a rule are not recognizable. In primitive therians such as e.g., Late Cretaceous eutherian *Barunlestes* (Fig. 4C) (Kielan-Jaworowska 1978) and Late Cretaceous metatherian *Asiatherium* (Szalay & Trofimov 1996 and personal observations), the vestigial radial condyle is still visible as a spherical structure, while the ulnar condyle cannot be distinguished, being confluent with the wall of the trochlea. In more advanced therians, even in scansorial forms, in which there is a strong degree of rotation of the antebrachium and manus, there is a trochlea, typical for the therian pattern of the elbow joint. The remnant of the radial condyle is still recognizable in the scansorial marsupial *Trichosurus* (Fig. 4A), while in the primate *Cercopithecus*, in spite of rotation in the elbow joint, the remnant of the radial condyle is hardly discernible (Fig. 4B). Comparison of *Trichosurus* with *Echinosorex* shows that in *Echinosorex*, which is terrestrial, there is no separate radial condyle (Table 1). The same is true of other extant terrestrial insectivorous mammals such as *Paraechinus* and *Erinaceus*, and rodents *Meriones*, *Rattus*, and *Citellus*, measured by us but not included in Table 1. In scansorial and in many other therians, on the radius there is an articular circumference which allows the rotation of the radius. In all other non-fossorial therians (except the Anthropoidea, in which, due to an increase of the manipulatory activity of the antebrachium and manus, there is a spherical radial condyle – capitulum), the radial condyle is not differentiated from the trochlea. The presence of a trochlea restricts the movements of the ulna to a plane perpendicular to the transverse axis of the elbow joint.

Fossorial Theria (e.g., Talpidae, Chrysochloridae, Spalacidae, Myospalacidae, and extinct Palaeanodonta) (Figs 2D–F, 5, 6, 7E–H, 8G–I). — It is generally accepted that abduction of the forelimbs during digging, which is characteristic of most fossorial Theria (but not e.g., of the Spalacidae) is secondary (see Gambaryan 1960 and Hildebrand 1988, for reviews). This means that fossorial Theria originated from forms with parasagittal limbs and a trochlea. In consequence we accept also that the radial condyle (capitulum), that occurs in the fossorial forms that abduct their forelimbs, made its appearance secondarily, in relation to the compulsion of rotation in the elbow joint. In these fossorial forms, including extinct palaeanodonts (Rose & Emry 1983; Rose *et al.* 1992 and references therein), adaptations for digging resulted in the formation of a radial condyle and retention of the trochlea. The ulnar condyle, however, did not reappear. As in all Theria (see above), the intertubercular groove in all fossorial therians is narrow.

Among the fossorial therians only the Talpidae acquired a fully sprawling stance of the forelimbs, which are oriented at 120–160° with respect to the sagittal plane. The glenoid fossa faces ventrally

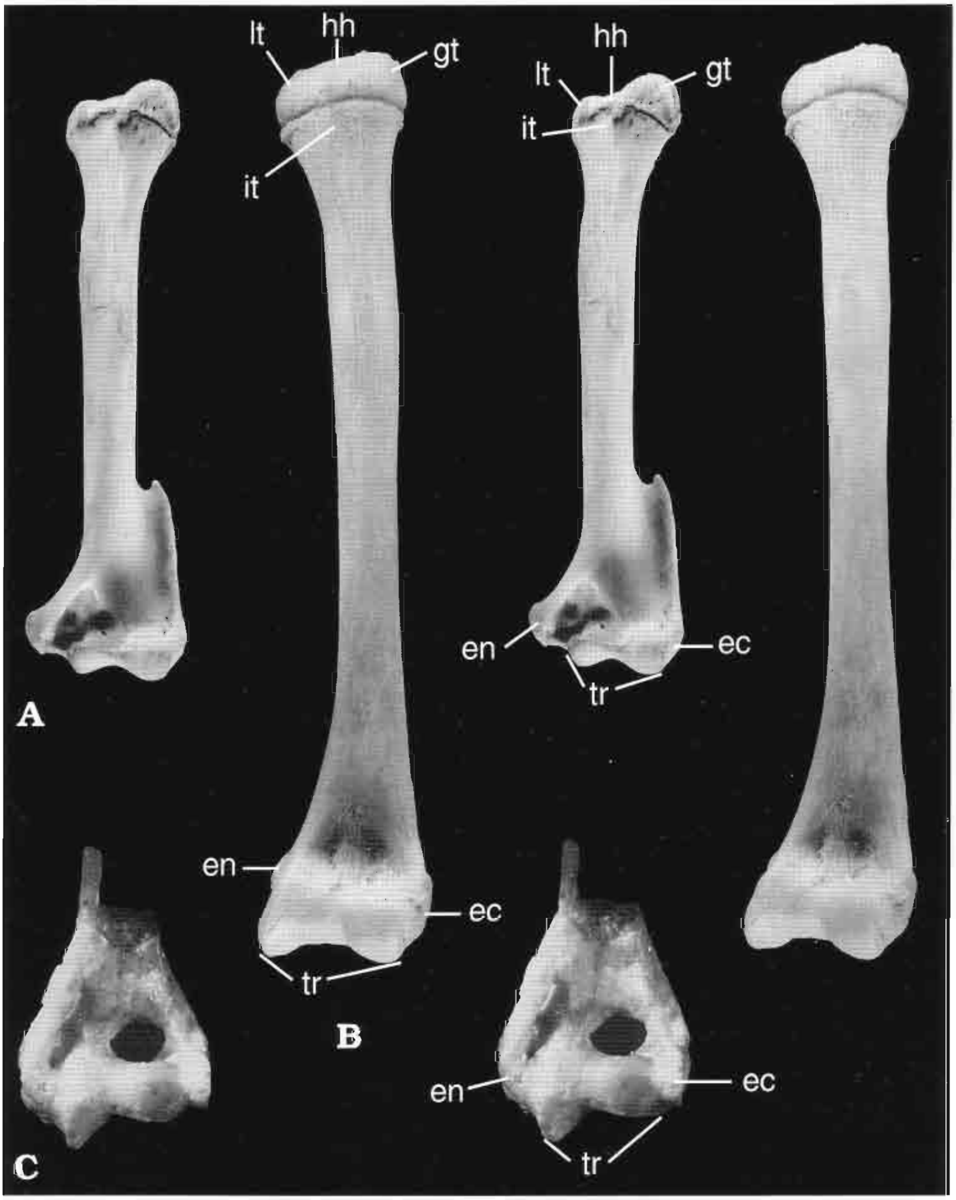


Fig. 4. Stereo-photographs of left humeri (**C** distal end only) in ventral view. **A**. *Trichosurus vulpecula*, Recent, ZIN 31713, × 1. **B**. *Cercopithecus* sp., Recent, ZIN – no number, × 1. **C**. *Barunlestes butleri* – vestigial radial condyle is seen on the right side of the trochlea, Late Cretaceous, Barun Goyot Formation, Mongolia, ZPAL MgM-I/77, × 6. ec – ectepicondyle, en – entepicondyle, gt – greater tubercle, hh – humeral head, it – intertubercular groove, lt – lesser tubercle, tr – trochlea. Above the trochlea in all three specimens there is a deepening of fossa coronoidea, partly broken in *Barunlestes*.

and is elongated anteroposteriorly. The proximal and distal ends of the humerus are expanded. The humeral head is narrow, allowing only flexion-extension, while rotation of the humerus is in the

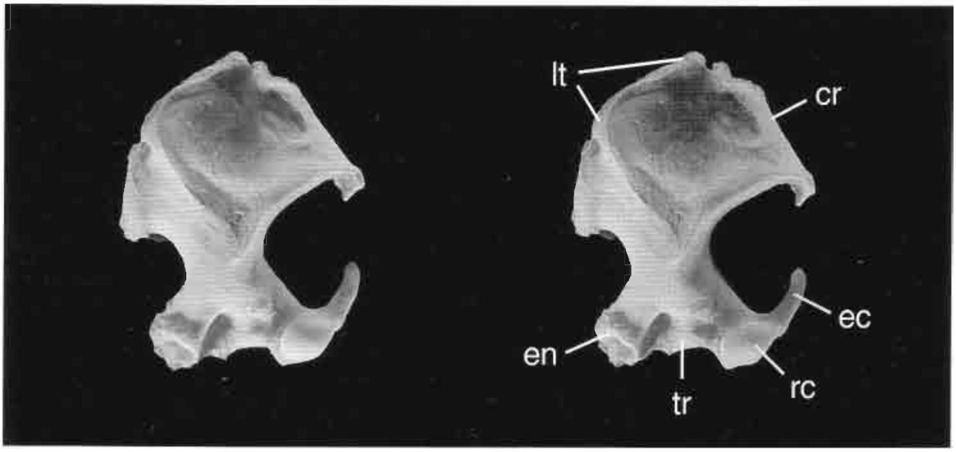


Fig. 5. *Talpa europaea*, Recent. Stereo-photograph of left humerus in ventral view, coated with ammonium chloride, ZPAL Mw-5, × 2.5. cr – crest of the greater tubercle, ec – ectepicondyle, en – entepicondyle, lt – lesser tubercle, rc – radial condyle, tr – trochlea.

humero-clavicular joint, which does not occur in other mammals (Gambaryan 1960). While the animal draws the soil aside, rotation takes place, and that is why the lesser tubercle is larger than the greater, as characteristic of animals with sprawling posture, but in contrast to the condition in non-fossorial Theria. There is no humeral torsion. The radial condyle is completely separated from the trochlea and very prominent in *Talpa*. In *Neurotrichus*, which belongs to the primitive Talpidae, and in which the abduction of the forelimbs is less advanced than in *Talpa*, the convexity of the radial condyle is smaller (Table 1). The changes in orientation of the manus require independent movements of radius and ulna. The presence of a spherical radial condyle, separated from the trochlea, ensures rotation of the radius about its longitudinal axis. The articulation of the radius and ulna is flat, allowing only for a small movement of the bones relative to each other, but not rotation (Gambaryan 1960 and references therein; Gambaryan & Gasc in preparation).

Chrysochloridae and Myospalacidae move their forelimbs posterolaterally during digging, and we refer to them as half-sprawling; this probably was also the case in extinct Palaeanodonta (Rose & Emry 1983; Rose *et al.* 1992). Chrysochloridae differ from the Talpidae and all other fossorial therians in having twisted humerus, the torsion of which amounts to about 60°. In Chrysochloridae the lesser tubercle is larger than the greater and the radial condyle is completely separated from the trochlea, as in other fossorial therians. The Chrysochloridae (Figs 7H, 8G) are similar to the Talpidae in the structure of the glenoid fossa, but differ in structure of the proximal and distal extremities of the humerus (Gasc *et al.* 1986).

The extinct Palaeanodonta resemble the Chrysochloridae in various adaptations for burrowing, but differ from them in having only very little humeral torsion (Rose & Emry 1983).

The structure of the glenoid fossa in Spalacidae (*Nannospalax*) and Myospalacidae is the same as in non-fossorial therians. These two fossorial families of Rodentia differ considerably from each other in the mode of burrowing, which results in a different structure of the distal extremity of the humerus (Fig. 6). In Spalacidae, whose humerus works in a parasagittal plane, there is only a trochlea, and the distal end of the humerus is not expanded; while in Myospalacidae, which abduct the forelimbs during digging, there is a separate radial condyle in addition to the trochlea, and the distal end of the humerus is strongly expanded (Gambaryan 1960; Gambaryan & Gasc 1993).

In spite of the abducted trajectory of digging in Myospalacidae, the lesser tubercle is smaller than the greater, as characteristic of mammals with parasagittal limbs, including Spalacidae. While in other tetrapods with abducted limbs medial rotation of the humerus takes place due to the action of mm.

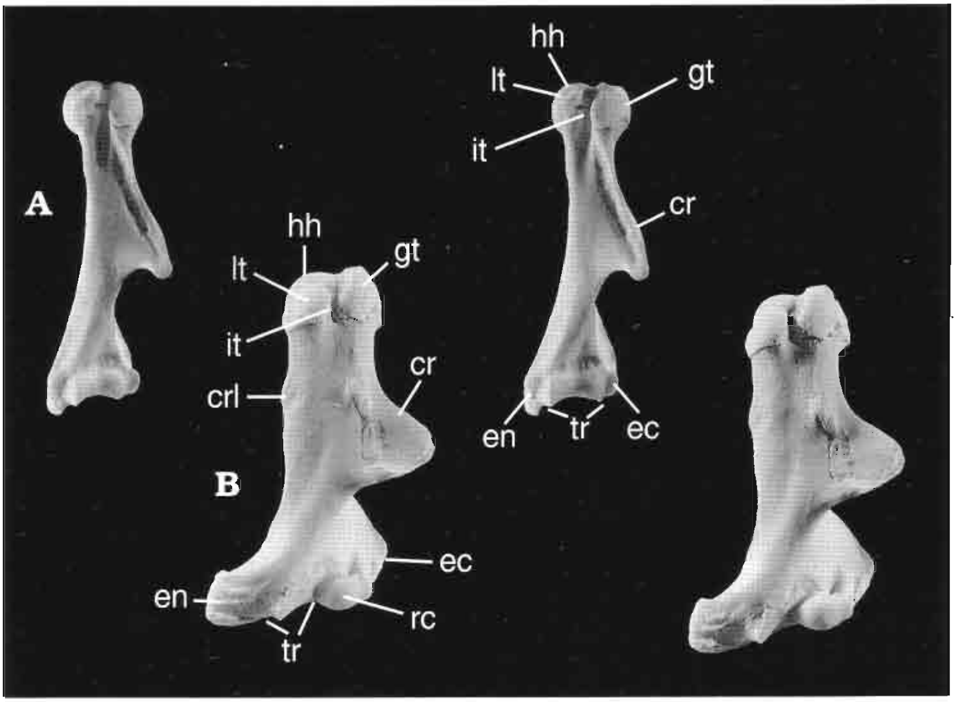


Fig. 6. Stereo-photographs of left humeri in ventral view. **A**. *Nannospalax nehringi*, Recent, ZPAL Mw-4, × 1.5. **B**. *Myospalax myospalax*, Recent, ZIN 386, × 1.4. Note than in *Nannospalax* (Spalacidae), whose forelimbs work in a parasagittal plane there is a trochlea and no radial condyle. In *Myospalax* (Myospalacidae) which abducts forelimbs, in addition to the trochlea there is a prominent radial condyle. cr – crest of the greater tubercle, crl – crest of the lesser tubercle, ec – ectepicondyle, en – entepicondyle, gt – greater tubercle, hh – humeral head, it – intertubercular groove, lt – lesser tubercle, rc – radial condyle, tr – trochlea.

subscapularis, proscapulohumeralis and pectoralis (in monotremes), or mm. subscapularis, scapulohumeralis posterior and pectoralis (in lacertilians), all of which insert on the lesser tubercle, in Myospalacidae the medial rotation is due to mm. latissimus dorsi and teres major which insert on the enlarged crest of the lesser tubercle (Fig. 6B).

The convexity of the radial condyle in all fossorial therians with half-sprawling stance studied by us is greatest at the beginning of the propulsive phase (Table 1 and Fig. 2, position 120°), which indicates that the mobility of the elbow joint was greatest at this stage. This shows also that the elbow joint is in the most flexed position at this stage. In *Talpa*, which has a sprawling stance, the greatest mobility (the greatest convexity of the radial condyle) occurs at the extended elbow joint (positions 30 and 60°).

Humerus structure in sprawling and parasagittal stance

The data presented in the foregoing chapter allow one to establish the list of features that distinguish the humeri in sprawling and parasagittal stance (Figs 3–8).

Torsion. — The torsion (or twisting) of the humerus was generally regarded as a very important character that allows distinction of the sprawling from the parasagittal

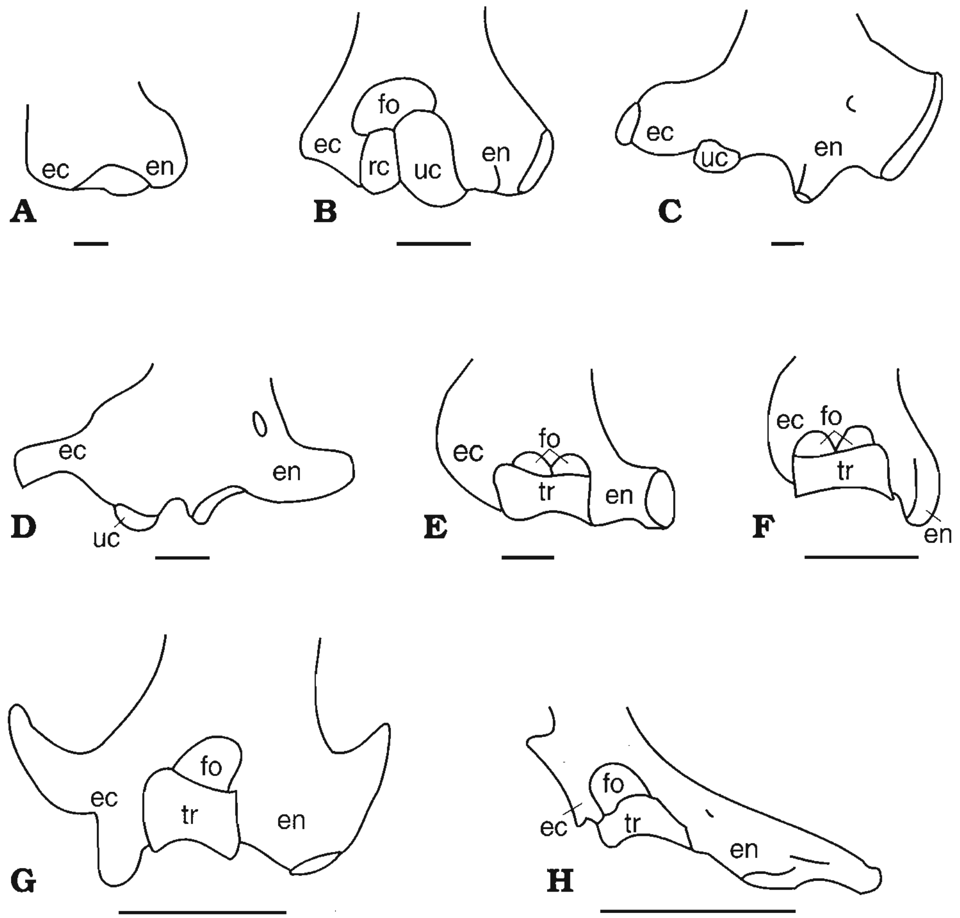


Fig. 7. Camera lucida drawings showing the distal ends of the humeri in dorsal view. **A**. *Varanus*, **B**. *Lambdopsalis*, **C**. *Tachyglossus*. **D**. *Ornithorhynchus*, **E**. *Myospalax*, **F**. *Nannospalax*, **G**. *Talpa*, **H**. *Chrysochloris*. ec – ectepicondyle, en – entepicondyle, fo – fossa olecrani, rc – radial condyle, tr – trochlea, uc– ulnar condyle. Scale bars are 5 mm, with except for *Chrysochloris* which is 2 mm.

stance in fossil mammals (e.g., Simpson 1928a; Lessertisseur & Saban 1967; Kielan-Jaworowska & Gambaryan 1994; Sereno & McKenna 1995). The data discussed above show that humeral torsion is indicative of the sprawling posture in animals that use symmetrical diagonal gaits; however, it does not occur in anurans which have a sprawling posture, but use asymmetrical jumps. Humeral torsion is high (60°) in Chrysochloridae, that secondarily acquired a half-sprawling posture, but very small or absent in other fossorial mammals that also secondarily acquired a half sprawling or sprawling (Talpidae) posture. It follows that lack of the torsion is not indicative of parasagittalism.

Condylar structure of the elbow joint. — In all extant vertebrates with primary abducted limb posture (Urodela, Anura, Lacertilia, Crocodylia, Monotremata) there are prominent, radial (capitulum) and ulnar condyles at the distal end of the humerus. A spherical radial condyle permits the rotation of radius about its longitudinal axis and

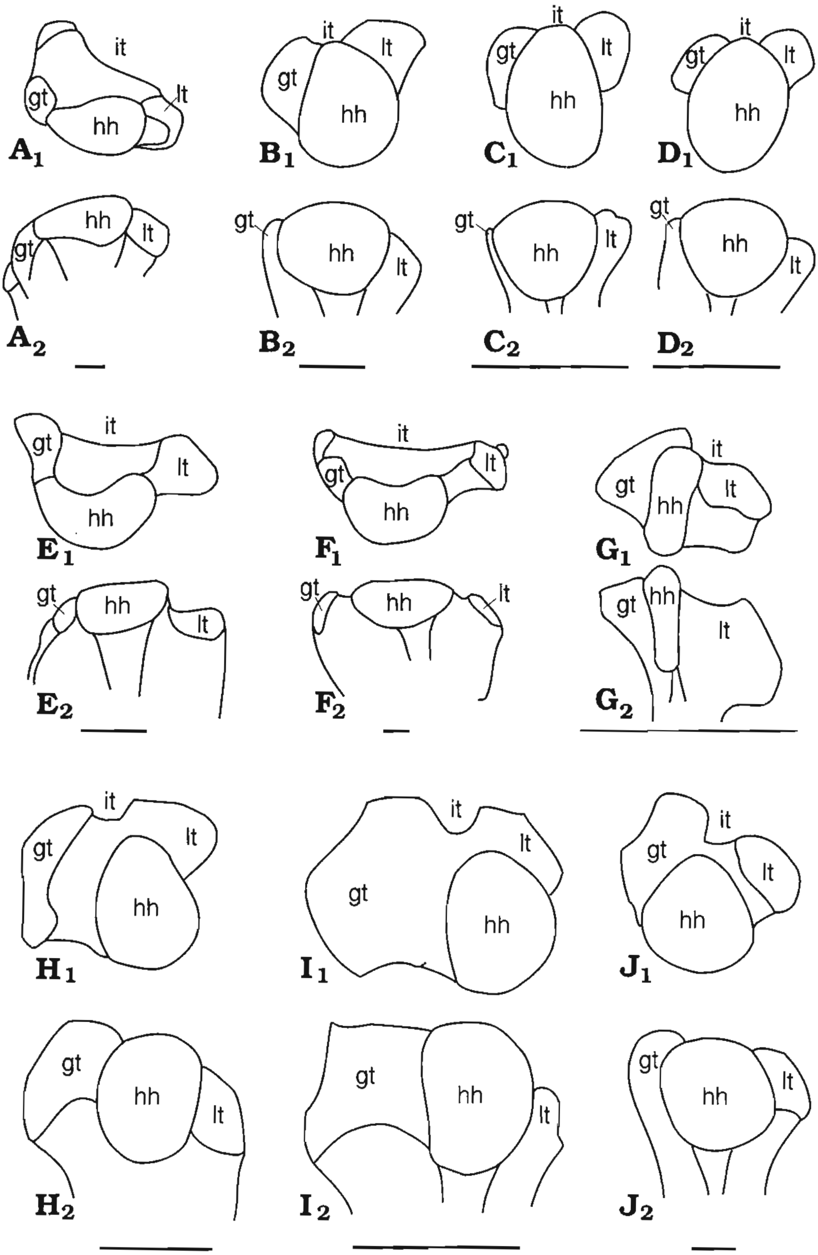


Fig. 8. Camera lucida drawings of the proximal parts of left humeri. **A1–J1** proximal views, **A2–J2** dorsal views **A**. *Varanus*. **B**. *Lambdopsalis*. **C**. *Nemegtbaatar*. **D**. *Chulsanbaatar*. **E**. *Ornithorhynchus*. **F**. *Tachyglossus*. **G**. *Chrysochloris*. **H**. *Myospalax*. **I**. *Nannospalax*. **J**. *Trichosurus*. gt – greater tubercle, hh – humeral head, it – intertubercular groove, lt – lesser tubercle. Scale bars are 5 mm, except for **D** and **G** which are 2 mm. Note that the lesser tubercle has greater transverse diameter than the greater tubercle in animals with abducted forelimbs (**A–G**), but smaller in animals with parasagittal limbs (**I**, **J**). In *Myospalax* which abducts its forelimbs, the lesser tubercle is smaller, as the rotary function of muscles that insert upon it, is replaced by muscles that insert on enlarged crest of the lesser tubercle (see Fig. 6).

adduction-abduction in the elbow joint. In specialized forms (monotremes, Fig. 3B, C) there is a conjoined radio-ulnar condyle, while in anurans the ulnar condyle is vestigial and an enormously enlarged radial condyle articulates with fused radius and ulna. In mammals with parasagittal limbs the condyles disappear and are transformed into a trochlea; however, a vestigial radial condyle may be recognized in some early therians or extant scansorial mammals (Fig. 4A, C, see also Jenkins 1973). In forms with a trochlea, the rotation of the radius is ensured by the movements in the shoulder joint, as all the movements of the forelimb are in the same plane. In fossorial forms which abduct their forelimbs during digging, or acquired a fully sprawling stance (Talpidae), a radial condyle developed secondarily in addition to the trochlea, but never an ulnar condyle. The ulnar condyle is necessary for abduction-adduction of the ulna; its lack is consistent with the presence of a trochlea, which restricts the movements of the ulna to one plane.

The condylar structure of the elbow joint, with a spherical radial and well defined ulnar condyle (or conjoined radio-ulnar condyle) and lack of a trochlea, is characteristic of primary sprawled forelimbs, while presence of a radial condyle and a trochlea is characteristic of secondary sprawled forelimbs.

Size of the lesser and greater tubercles. — In forms with primary abducted forelimbs, e.g., in lacertilians, cynodonts, morganucodontids and monotremes, the lesser tubercle is wider and protrudes more strongly over the shaft of the humerus (medially) than the greater tubercle (Fig. 8A–G, see also Jenkins 1971b; Jenkins & Parrington 1976). In mammals with parasagittal limbs the lesser tubercle is smaller (and narrower) than the greater tubercle. In some, but not all burrowing mammals with sprawling forelimbs (Talpidae), and those with half sprawling forelimbs (Chrysochloridae), the size of the lesser tubercle increases and it becomes larger than the greater tubercle. This difference between sprawling and parasagittal limbs is related to different movements of the humerus in the shoulder joint. In forms with sprawling limbs, during the propulsive phase there occurs medial rotation of the humerus in the shoulder joint, caused by the action of mm. subscapularis and scapulohumeralis posterior, which insert on the lesser tubercle. An increase of the size of these muscles reflects in an increase of the transverse diameter of the lesser tubercle. This character, however, is equivocal, for e.g., in Myospalacidae, which abduct their forelimbs, the greater tubercle is larger than the lesser tubercle (Fig. 6B), and rotation of the humerus is due to the action of mm. latissimus dorsi and teres major which insert on an enlarged crest of the lesser tubercle. The larger transverse diameter of the lesser tubercle than of the greater tubercle is indicative of the primary sprawling stance. It occurs also in most fossorial therians which secondarily acquired a semi-sprawling or sprawling stance, with exception of the Myospalacidae.

Width of the intertubercular groove. — In tetrapods with sprawling stance, several muscles that originate on the coracoid bone and sternum pass along the wide intertubercular groove. In therians, the intertubercular groove is narrow, as only the tendon of m. biceps brachii caput longum passes along the groove. A wide intertubercular groove is indicative of primary sprawling stance; a narrow groove is indicative of parasagittal stance. In fossorial therians which secondarily acquired a sprawling or semi-sprawling stance, the intertubercular groove is narrow.

Forelimb structure in multituberculates

(Figs 1, 2B, 7B, 8B–D, 9)

The multituberculate glenoid fossa has been described by McKenna (1961), Deischl (1964), Krause & Jenkins (1983), Kielan-Jaworowska & Gambaryan (1994) and Sereno & McKenna (1995). As stated by Krause & Jenkins (1983: p. 209): 'The glenoid is a shallow, pyriform fossa, broadest posteriorly and tapering towards the coracoid suture [...] The scapular and coracoid parts of the glenoid [...] form an arcuate (approximately 90°) surface to receive the humeral head'. The scapular spine is not situated in the middle of the lateral side of the scapular blade (as in therian mammals), but very close to its anterior margin. In front of it, there is an incipient supraspinous fossa (Kielan-Jaworowska & Gambaryan 1994). The infraspinous fossa is deep and relatively large. The medial part of the scapula (fossa subscapularis) is convex, its arc being 120° (Kielan-Jaworowska & Gambaryan 1994).

The multituberculate humeri, figured or described by Gidley (1909), Simpson (1928a), Deischl (1964), Sahni (1972), Jenkins (1973), Kielan-Jaworowska & Dashzeveg (1978), Krause & Jenkins (1983) and Kielan-Jaworowska (1989), are incomplete. The only complete multituberculate humeri described so far are: (1) two isolated bones, IVPP V9051 and IVPP V8408, from the Early Eocene Bayan Ulan Formation of China, identified by Kielan-Jaworowska & Qi (1990) as ?*Lambdopsalis bulla* (see also Kielan-Jaworowska & Gambaryan 1994), and (2) two humeri belonging to the same individual, PSS-MAE-103, of *Bulganbaatar nemegtbaataroides* from the Late Cretaceous Djadokhta Formation at Bayn Dzak in Mongolia, found in association with the skull, pectoral girdle and other parts of the forelimbs (Sereno & McKenna 1995).

The multituberculate humeri vary in proportions, from relatively slender ones, such as *Kryptobaatar saichanensis* (originally referred to *Tugrigbaatar* by Kielan-Jaworowska & Dashzeveg 1978) and *Bulganbaatar nemegtbaataroides* (Sereno & McKenna 1995), to more robust such as *Lambdopsalis bulla* (Kielan-Jaworowska & Qi 1990; Kielan-Jaworowska & Gambaryan 1994, and Fig. 9). In all the humeri, their proximal and distal epiphyses are expanded, and as a rule the distal more strongly than the proximal. The degree of torsion in *Lambdopsalis*, in IVPP V8408 is 38° and in IVPP V9051 is 24°. Kielan-Jaworowska & Gambaryan (1994) attributed the differences between the two humeri of *Lambdopsalis* to individual age and the inaccuracy of gluing. However, reexamination of the specimens shows that there is indeed a difference between the degrees of torsion. Both humeri fit best into the size of *Lambdopsalis* (Miao 1988). Given that there is a high variation in the degree of torsion in Monotremata, one can accept that similar variation may have existed in *Lambdopsalis*.

The humerus of *Kryptobaatar saichanensis* is known from two large fragments, on the basis of which we tentatively estimate its degree of torsion as about 30°. In *Bulganbaatar* the torsion is only 15° (Sereno & McKenna 1995). Deischl (1964) calculated the degree of torsion in multituberculate humeri to be 70°, which is higher than estimated by us for any taxon.

The humeral head is spherical and strongly overhangs the shaft dorsally; its articular surface faces more proximally than dorsally (as in graviportal mammals), which means that it is larger in proximal than in dorsal view (Fig. 8B–D). Such structure of the humeral head indicates the ability for stretching the forelimbs. The lesser tubercle is slightly lower than the greater tubercle, but its transverse diameter is larger. It is placed further away from the middle of the humeral head than the greater tubercle. The intertubercular groove is very wide in multituberculates examined by us. In incomplete humeri of the Late Cretaceous Mongolian taxa the width of the intertubercular groove (Kielan-Jaworowska, 1989; Kielan-Jaworowska & Gambaryan 1994: figs 16E and 23E) amounts to 30% of the proximal epiphysis in *Nemegtbaatar*, ZPAL MgM-I/81, about 40% in *Chulsanbaatar*, ZPAL MgM-I/83, and 40% in an unidentified multituberculate from the Djadokhta Formation, ZPAL MgM-I/165. In the unidentified humerus from the Coniacian of Uzbekistan, figured by Kielan-Jaworowska & Nessov (1992: fig. 5A), the intertubercular groove amounts to 39% of the proximal epiphysis. The width of the intertubercular groove is 28% and 31% of the width of the proximal epiphysis in two specimens of *Lambdopsalis* (Fig. 9). Sereno & McKenna (1995) refer to the groove in *Bulganbaatar* as wide,

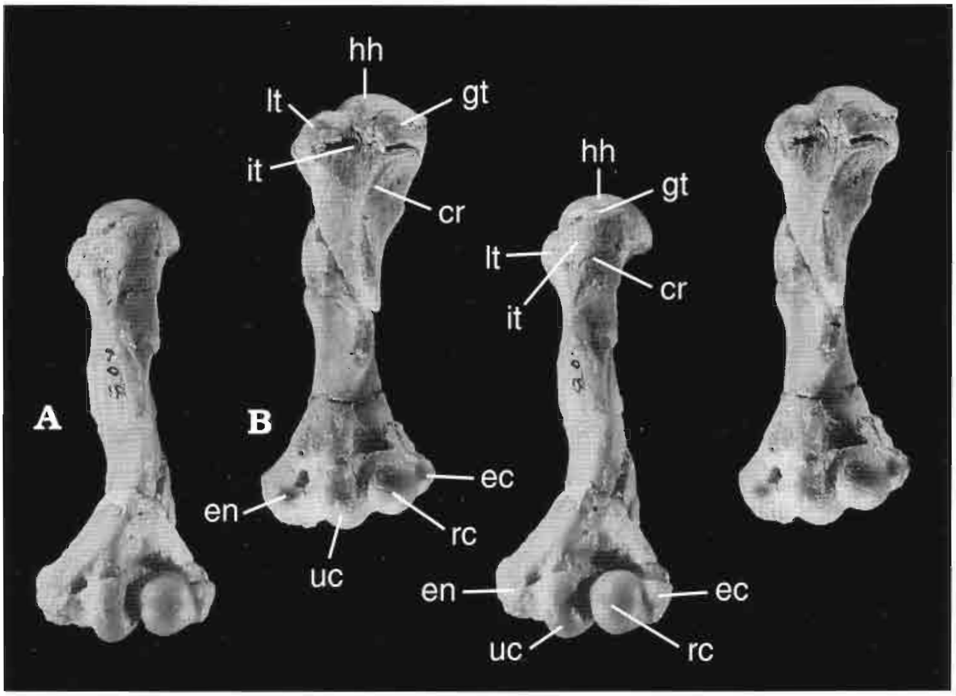


Fig. 9. *Lambdopsalis bulla*, Eocene, Bayn Ulan Beds, Bayan Ulan, China. Stereo-photographs of left humeri in ventral view, × 1.5. **A**. IVPP V8408. **B**. IVVP V9051. Fossa coronoidea is seen in both specimens above the condyles. cr – crest of the greater tubercle, ec – ectepicondyle, en – entepicondyle, gt – greater tubercle, hh – humeral head, it – intertubercular groove, lt – lesser tubercle, rc – radial condyle, uc – ulnar condyle.

but it appears narrow in their fig. 3e. However, on the copy of the original of the drawing (kindly sent to us by Paul Sereno) it is wide, similar to that in other multituberculates. The crest of the greater tubercle in multituberculates is prominent.

The distal epiphysis is expanded in all known multituberculate humeri, perhaps being the narrowest in *Bulganbaatar*, if correctly reconstructed by Sereno & McKenna (1995: fig. 3). Its characteristic feature is the presence of a very large, spherical radial condyle, delimited by a deep intercondylar groove from the prominent ulnar condyle. The ulnar condyle is narrower than the radial condyle and in ventral view more elongated longitudinally; there is a longitudinal crest that extends along its longitudinal axis. The differences between the angles of convexity of the radial and ulnar condyles are very small in multituberculates, while in other tetrapods with primary abducted forelimbs (but not in monotremes), the ulnar condyle is much less convex (Table 1 and Fig. 2A–C). In all known multituberculate humeri there is no trace of even an incipient trochlea (*contra* Sereno & McKenna 1995), the entepicondyle is large, the ectepicondyle smaller. Among all studied tetrapods, only in multituberculates do the radial and ulnar condyles extend from the ventral to the dorsal surface of the humerus (Figs 1A, 2B, 7B, 9).

In the multituberculate ulna, the olecranon is very extensive, relatively larger than typical for Theria, and it approaches the size in some non-specialized fossorial forms, such as *Ellobius* and *Prometheomys* (Gambaryan 1960). As noted by Krause & Jenkins (1983), the medial margin of the olecranon apex bears a small excrescence, also seen in the ulna of an unidentified multituberculate AMNH 118267, figured by Kielan-Jaworowska & Gambaryan (1994: fig. 14D). In the semilunar notch there is a longitudinal concave facet for the ulnar condyle of the humerus, separated by a prominent ridge from the shallow and concave radial notch (Kielan-Jaworowska & Gambaryan 1994: fig. 16D, E). The ridge that separates the ulnar condyle from the radial notch articulates with the intercondylar groove on the humerus. The head of the radius is elliptical, longer anteroposteriorly than transversely, and bearing a spheroidal concave facet that articulates with the radial condyle. On the medial side of the proximal part there is a facet – articular circumference (Kielan-Jaworowska & Gambaryan 1994: fig. 14A), for articulation with the ulna.

Evaluation of Sereno & McKenna hypothesis

Sereno & McKenna (1995) suggested that multituberculate posture was parasagittal, similar to that of *Didelphis*. They based their hypothesis on the structure of the shoulder girdle and forelimbs in *Bulganbaatar*, the humerus of which shows a small degree of torsion (15°), on the structure of the distal end of the humerus, and the structure of the glenoid fossa. Sereno & McKenna (1995: p. 146) argued that the parasagittal position of multituberculate forelimbs is indicated by: 'marked ventral (not lateral) orientation of the glenoid, reduction in size of humeral epicondyles, and hinge-like form of the elbow joint (suggested by prominent, narrow ulnar condyle and broad intercondylar groove on the distal end of the humerus, approaching the form of the therian trochlear joint)'.

As discussed above and exemplified by Anura, Talpidae and Myospalacidae, the lack of humeral torsion does not necessarily imply parasagittal position of the forelimbs. We disagree with Sereno & McKenna's (1995) interpretation of the structure of the distal end of the multituberculate humerus. In various Late Cretaceous and Paleocene multituberculate humeri examined by the second author, and figured e.g., by Deischl (1964), Jenkins (1973), Kielan-Jaworowska & Dashzeveg (1978), Krause & Jenkins (1983), Kielan-Jaworowska & Qi (1989), and Kielan-Jaworowska & Gambaryan (1994), the intercondylar groove is narrow, both condyles are convex and the radial condyle is spherical. A sharp ridge in the semilunar notch of the ulna, that divides the articular surface for the ulnar condyle from the radial notch (e.g., Jenkins 1973: fig. 22; Krause & Jenkins 1983: fig. 13C; Kielan-Jaworowska & Gambaryan 1994: fig. 14D, E) indicates the presence of a narrow intercondylar groove. Such a ridge does not occur on the ulnae of therian mammals with a trochlea, except for some fossorial forms, in which the radial condyle is present (personal observations, see also Lessertisseur & Saban 1967 and Jenkins 1973: fig. 23).

In specialized fossorial mammals such as monotremes and various fossorial therians that abduct their forelimbs during digging, the distal end of the humerus, and especially the entepicondyle, is strongly expanded (Figs 3B, C, 6B, and 7C–H). In nonfossorial therians, on the contrary, the distal end of the humerus usually is hardly expanded and the epicondyles are small (Figs 4, 5A). Sereno & McKenna (1995) referred to the multituberculate epicondyles as 'reduced in size'. However, the distal end of multituberculate humerus is expanded and the entepicondyle, measured in ventral view, extends for 28–40% of the epiphysis width in various taxa figured by Krause & Jenkins (1983), Kielan-Jaworowska & Qi (1990), Kielan-Jaworowska & Gambaryan (1994), and Sereno & McKenna (1995), while the ectepicondyle is distinctly smaller.

We accept the ventral orientation of the glenoid fossa in *Bulganbaatar* recognized by Sereno & McKenna (1995), but such a position does not necessarily indicate parasagittalism, as it occurs also in forms with abducted limbs, e.g., in the Talpidae.

In order to test the parasagittal position of the forelimbs in multituberculates, we studied the possible movements in the shoulder joint of *Nemegtbaatar gobiensis* (ZPAL MgM-I/81), in which the scapula with glenoid fossa and proximal part of the humerus have been found in association (Fig. 1C). In *Didelphis* the range of excursion of the humerus in flexion-extension in the shoulder joint is 70° (140–70°) in propulsive phase and up to 60° in swing phase (Jenkins & Weijs 1979). In *Nemegtbaatar* the maximum excursion of the humerus is 50° (160–110°). This shows that the range of the humeral excursion is much smaller in *Nemegtbaatar* than in *Didelphis*. The orientation of multituberculate humeral head, discussed on p. 31, shows that during the swing phase the forelimbs were stretched anteroventrally, as characteristic of mammals before landing (Gambaryan 1974). This indicates that multituberculates were adapted for jumps as a mode of locomotion, rather than that they moved similarly to *Didelphis*.

In order to verify the opinion of Sereno & McKenna (1995: p. 147) that: '[...] a mobile pectoral girdle and shoulder joint and a forelimb posture with the elbow near the body wall arose only once, some time before the Late Jurassic, in a common ancestor of multituberculates, therians and their extinct allies' we compare the humeri in early therians and multituberculates.

In a symmetrodont from the Late Jurassic of Western Liaoning, China (Li *et al.* 1995) there is an incipient trochlea and prominent radial condyle, larger than in *Barunlestes* (personal information from Professors Chankuei Li and Yaoming Hu, letter of October 31, 1996). Krebs (1991) mentioned the presence of a trochlea in the Kimmeridgian 'eupantothere' *Henkelotherium*; however, examination of his fig. 8 shows the presence of both ulnar and radial condyles, in addition to which a trochlea might be present. The shoulder girdle is built on a modern therian pattern, consisting only of a scapula, with wide supraspinous fossa and coracoid process, and a clavicle. Rougier (1993) described the postcranial skeleton of an Early Cretaceous prototribosphenid *Vincelestes*, which has a distinct trochlea in addition to prominent radial and ulnar condyles. The intertubercular groove is very wide, and the degree of torsion is 40°.

In the Late Cretaceous metatherian *Asiatherium* (Szalay & Trofimov 1996) in addition to the trochlea there is a vestigial radial condyle. In the Early Cretaceous (Aptian or Albian) fauna of Khoboor in Mongolia, housed in the Palaeontological Institute in Moscow, there are numerous as yet undescribed postcranial fragments, examined by us, among which there are distal ends of therian humeri with a well developed trochlea and vestigial radial condyle. In the oldest described eutherian humerus of the Late Cretaceous *Barunlestes* there is a well developed trochlea and a vestigial radial condyle (Fig. 4C), much less prominent than in all known multituberculate humeri, including *Bulganbaatar*. The humerus of a Paleocene therian described by Jenkins (1973), not only acquired a trochlea, but also lost a vestige of the radial condyle. Its structure is similar to those in advanced therians.

The trochlear structure of the humeri of Cretaceous (Fig. 4C) and Paleocene therians (Jenkins 1973) is very different from that of the humeri of various Paleocene multituberculates (e.g., Krause & Jenkins 1983; Kielan-Jaworowska & Qi 1990 and

Figs 7B and 9 in this paper), which show a condylar structure. While in therians a trochlea is well developed in Early Cretaceous forms and possibly made its appearance during the Late Jurassic, it has not been acquired in the evolution of multituberculates.

In reply to critiques by Presley (1995) and Rougier *et al.* (1996), Sereno & McKenna (1996: p. 406) argued that: "As evidence against the therian-like structure and function of the multituberculate pectoral girdle and hind limb they [Presley and Rougier *et al.*] cite the greater degree of torsion in the shaft of another multituberculate (*Lambdopsalis* [...]). Marked humeral torsion and fossorial habits, however, are clearly correlated among mammals (for example, moles [sic] among living therians). Increased humeral torsion in this avowed fossorial multituberculate from the Paleogene can thus not be interpreted with confidence as a 'residuum of the primitive torsion between the humeral head and elbow condyle'[...]."

The reply of Sereno & McKenna (1996) implies that primitively multituberculates acquired a parasagittal position (apparently with a trochlea) while the abducted position in *Lambdopsalis*, as demonstrated by marked torsion of its humerus is secondary and due to its fossorial habits. Let us compare the structure of the humerus of *Lambdopsalis* with those of fossorial therian mammals. There is no humeral torsion in the Talpidae, but among extant fossorial therians there is a torsion of about 60° in Chrysochloridae. More important, however, is that in all fossorial therians, which secondarily abduct their forelimbs during digging, or acquired fully sprawling stance (Talpidae), the distal end of the humerus looks very different from that in *Lambdopsalis* (Figs 5–7, 9, see also Rose *et al.* 1992 and references therein). In fossorial therians there is a distinct radial condyle, in addition to the trochlea, but no an ulnar condyle, characteristic of multituberculates and other tetrapods with primary abducted forelimbs. It cannot be excluded that the notable torsion of the humerus in *Lambdopsalis* may have increased because of its semi-fossorial habits; however, there is no doubt that the condylar structure of the distal end of the humerus, characteristic for all multituberculates, with prominent radial and ulnar condyles, is primitive for mammals, as was convincingly demonstrated by Jenkins (1973).

Another source of evidence in establishing the sprawling *versus* parasagittal positions of the forelimbs in multituberculates may come from an analysis of the hind limb posture. In mammals (except for specialized fossorial forms), either both fore- and hind limbs are sprawled (monotremes) or parasagittal (therians). Some fossorial therians acquired a sprawling (Talpidae) or half-sprawling (Chrysochloridae and Myospalacidae) position of the forelimbs, while the hind limbs remained parasagittal.

Gambaryan & Kielan-Jaworowska (1995) argued that the deep multituberculate pelvis (different from that in therians) with femoral adductors originating ventral (not posteroventral as in therians) to the acetabulum and the mediolateral diameter of the tibia larger than the anteroposterior, indicate abduction of the femora by 30–60°. Also the structure of the multituberculate pes, with Mt III abducted by 30° from the longitudinal axis of the tuber calcanei, would be ineffective in parasagittal limbs, where the main axis of the pes extends in a parasagittal plane. Unusually long transverse and spinous processes of the lumbar vertebrae in multituberculates cannot be interpreted except than as an adaptation to asymmetrical gaits and steep jumps. In light of the above data the parasagittal position of multituberculate forelimbs does not hold.

Reconstruction of forelimb movements in multituberculates

The hypothesis of the parasagittal position of multituberculate forelimbs (Sereno & McKenna 1995) cannot be accepted in view of the anatomical evidence and failure of an attempt at reconstruction of parasagittal movements of the humerus in the glenoid fossa. We accept that multituberculates had a sprawling posture (Kielan-Jaworowska & Gambaryan 1994) and we shall try to reconstruct the movements of their forelimbs according to the premises of this idea (Fig. 10).

In tetrapods with a ventrally oriented glenoid fossa, abduction may be ensured by the rotation of the humerus, or by rotation of the scapula. The multituberculate scapula, which is narrow, with a convex medial surface, indicates that the scapula apparently rotated about its longitudinal axis more than in extant therians in which the scapula is wide and flat.

The humeral head in multituberculates is more spherical than in any extant small therian mammal. We measured the three angles of the convexity of the head (as described on p. 17) in seven taxa of extant therian mammals and found the greatest angles in scansorial forms, in *Cercopithecus* (50–75–123°), and in *Trichosurus* (51–105–114°), while in *Eosorex*, *Paraechinus*, *Nannospalax*, *Myospalax* and *Citellus* the angles in the third position were below 105°. In two specimens of *Lambdopsalis* the respective angles are 130–145–165° (IVPP V8408), 125–150–156° (IVVP V9051); 108–110–143° in *Nemegtbaatar* (ZPAL MgM-I/81); 127–150–160° in *Chulsanbaatar* (ZPAL MgM-I/83); 140–153–170° in a taeniolabidoid gen. et sp. indet. (ZPAL MgM-I/165).

The high convexity of the humeral head increases the possibility of humeral rotation, as the coracoid process could move transversely across the humeral head (changing its orientation with respect to the long axis of the humerus), while remaining always opposite the intertubercular groove (Fig. 1C). The high convexity of the humeral head in multituberculates shows that the humerus rotated during the propulsive phase, which is necessary for animals with abducted forelimbs.

We made an attempt to reconstruct the rotation of the humerus in the shoulder joint (Fig. 1C). If the scapula remained immobile, the humeral head could rotate only for 20°, as during further rotation the coracoid process would interfere with the lesser tubercle. If the scapula moved parallel to the longitudinal axis of the glenoid fossa, transversely across the humeral head, the rotation of the humerus would increase by 10°. If one accepts that the scapula, in addition to parallel movement, also rotated about its longitudinal axis, then the rotation of the humerus would increase for a further 15° or more. This would result in rotation of the humerus for at least 45°. In walking *Didelphis*, during the propulsive phase, the scapula rotates about its longitudinal axis, approximately 10° (personal observations of the first author, see also Jenkins & Weijs 1979). Thus rotation of the multituberculate scapula was probably greater than in *Didelphis*.

In Fig. 10, we present a reconstruction of the movements of the multituberculate antebrachium during the propulsive phase. Gambaryan & Kielan-Jaworowska (1994), on the basis of an analysis of the structure of the lumbar vertebrae and hind limbs, argued that multituberculates possibly had a steeper trajectory of jump than modern

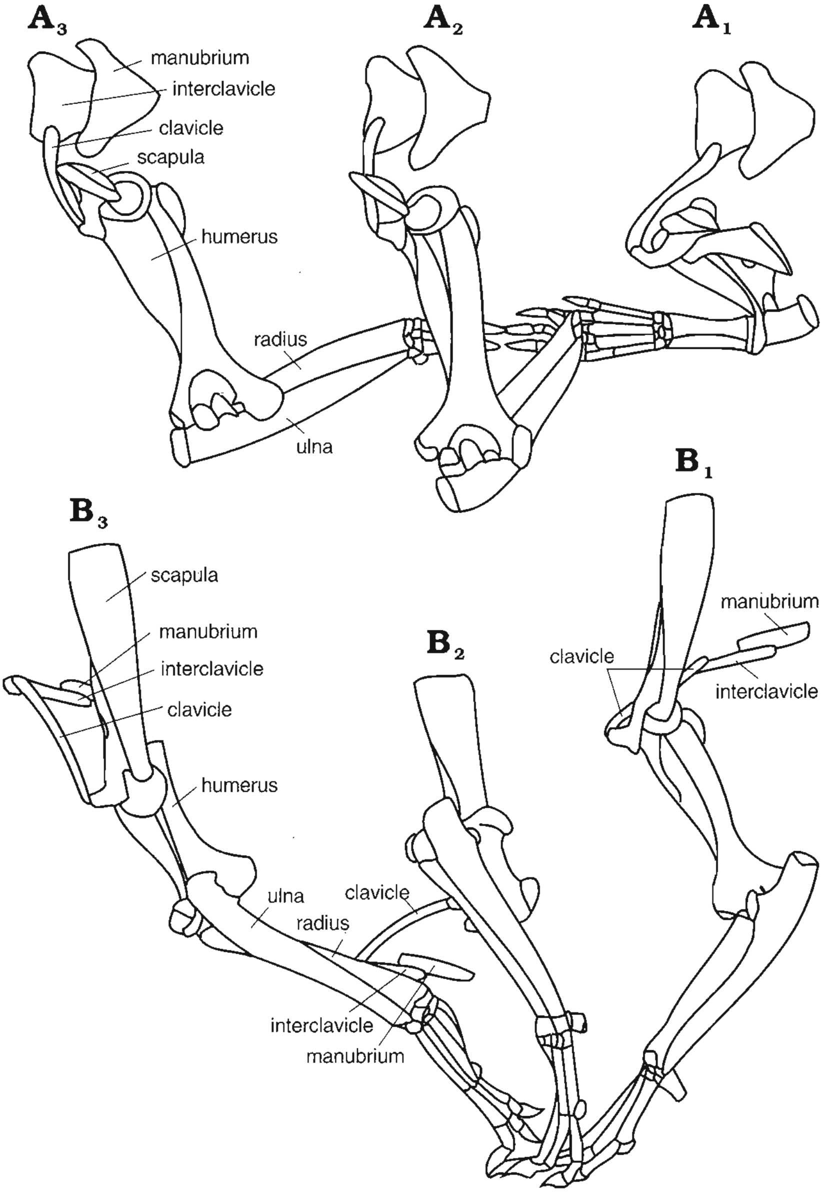


Fig. 10. Reconstruction of the forelimb movements during the propulsive phase in multituberculates, based on *Lambdopsalis*, *Nemegtbaatar*, and *Bulganbaatar* (Sereno & McKenna 1995: fig. 3). **A** – dorsal view, **B** – lateral view, **A**1, **B**1 – beginning, **A**2, **B**2 – middle, **A**3, **B**3 – end of the propulsive phase.

therians and that the forelimbs worked mostly to absorb the shock of landing. This implies that before landing the multituberculate forearms stretched strongly anteroventrally, as during jumps of extant therians (Gambaryan 1974: fig. 152). As discussed on pp. 31 and 34, this assumption is now confirmed by the structure of humeral head and shoulder joint. In Fig. 10 we show three stages of propulsion. The early stage (Fig.

$10A_1$, B_1) illustrates the moment of landing, during which the humerus was oriented more sagittally than in the successive stages, as characteristic of anurans (Gray 1968; Emerson 1983). Between the early and the middle stage of propulsion (Fig. $10B_1$, B_2) we reconstruct the body as falling down between the limbs, as characteristic of jumps of mammals and anurans (Gray 1968; Gambaryan 1974). At the same time the humeral head was depressed and occupied a position below the level of the elbow joint.

In multituberculates (and in anurans), which land simultaneously on both forelimbs, there is no undulation of the body, and there occurs a strong flexion of the elbow joint. Landing on both forelimbs resulted in lateral movement of the elbow joint in multituberculates, in relation to which the flexion of the elbow joint increased (Fig. $10A_2$). This contrasts with the movements in tetrapods which use symmetrical, diagonal gaits (Urodela, Lacertilia, Crocodylia and Monotremata), where the humerus is oriented horizontally during all the stages of the propulsive phase. In these forms there is very little flexion of the elbow joint, because this is compensated for by undulations of the body.

Between the middle and end of the propulsive phase (Fig. $10B_2$, B_3) the body elevated between the forelimbs, but not as high as at the beginning (B_1), the humerus was situated not so close to the sagittal plane as at the beginning, and the sternum was situated lower than at the beginning of the propulsive phase. Further elevation of the sternum was due to the action of the hind limbs. At the end of the propulsive phase (Fig. $10A_3$) the humerus was more abducted than at the beginning.

Absorption of the shock of landing in mammals involves different elements of the shoulder girdle and forelimb. The elbow joint plays an important role in this absorption; during landing it flexes, while m. triceps brachii (one head of which originates on the scapula and two on the humerus, and it inserts on the olecranon) acts against the flexion. Increase of the size of the olecranon plays an important role in increasing the moment arm of m. triceps brachii. As discussed above, the olecranon is very large in this group.

During the propulsive phase (Fig. 10A) the olecranon is inclined towards the ectepicondyle. M. epitrochleoanconeus, which originated on the dorsal surface of the entepicondyle and inserted on the excrescence on the olecranon apex, prevented extensive inclination of the olecranon. When during landing the forelimbs were stretched anteroventrally, the elbow joint extended and the olecranon fitted into a deep fossa olecrani on the dorsal side of the humerus (Fig. 7B). Strong flexion of the elbow joint during the middle of the propulsive phase, required a deep coronoid fossa on the ventral side of the humerus, into which fitted the radial head (Fig. 9).

Strong flexion-extension movements of the elbow joint are characteristic also of all the Theria with parasagittal forelimbs (Gambaryan 1974). Although the stance of therian and multituberculate forelimbs is different, the strong flexion-extension of the elbow joint in both groups resulted in formation of a fossa olecrani (Fig. 7) which does not occur in other tetrapods with abducted forelimbs.

As discussed above, the action of the forelimbs varies in forms with sprawling posture. While in e.g., *Varanus* the humerus retracts up to 135° during the propulsive phase, in *Tachyglossus* there is almost no retraction. The only character that occurs constantly in all the tetrapods with abducted limbs is the presence of the radial condyle. The spherical structure of the radial condyle is characteristic of forms with primary abducted forelimbs, and its mean convexity is similar even in forms which move differently, it is e.g., 135° in *Varanus*, and 127° in *Tachyglossus*; in forms with secondarily abducted forelimbs the mean convexity is e.g., 130° in *Talpa* and 136° in *Chrysochloris* (see Table 1).

The spherical structure of the radial condyle alone (without data on the structure of the head of the radius and the articular surface for the ulnar condyle on the ulna) does not specify the maximum mobility of the elbow joint. However, an analysis of Table 1 and Fig. 2 indicates in which position of the elbow joint the mobility is the greatest. The most extended position of the elbow joint in multituberculates is at 0° and the most flexed at 120°. In all multituberculates the least mobility of the antebrachium is at the position 60°. This shows that the greatest rotation of the antebrachium occurred at the beginning and at the end of the propulsive phase.

The rotation of the radius about its longitudinal axis in multituberculates is greater than in other extant tetrapods with sprawling posture studied by us. We measured the angle of the arc of the articular circumference on the radius in *Nemegtbaatar* ZPAL MgM-I/81 (Kielan-Jaworowska & Gambaryan 1994: fig. 14A) which is 120°, while the angle of the concave surface of the ulna which articulates with the radius, is 50° (the ulna in this specimen has been broken at the level of the radial notch and allowed us to take these measurements). It follows that the free part of the arc of the articular circumference along which the radius may rotate has an angle of 70°. Multituberculates are unique among terrestrial tetrapods with sprawling posture in that they have a large spherical radial condyle and at the same time a large articular circumference.

Conclusions

Testing the hypotheses of Sereno & McKenna (1995) on multituberculate parasagittal stance and of Kielan-Jaworowska & Gambaryan (1994) on sprawling stance, using anatomical comparisons and reconstruction of multituberculate forelimb movements, leads to the following conclusions.

In terrestrial tetrapods with a primary sprawling posture, which use symmetrical diagonal gaits (Urodela, Lacertilia, Crocodylia, and Monotremata), the humerus shows a relatively high torsion (up to 60°), wide intertubercular groove, lesser trochanter wider than the greater one, and the condylar type of the elbow joint, with spherical radial condyle and oval, convex ulnar condyle. Abducted forelimbs occur also in Anura, which use asymmetrical jumps and have a straight humerus (without torsion). Therian mammals acquired a trochlea probably during the Late Jurassic. They retained a vestigial radial condyle in Late Cretaceous forms, but lost this condyle in the Paleocene. Fossorial mammals that secondarily acquired half-sprawling or sprawling stance differ from tetrapods with primary sprawling stance in having a trochlea and radial condyle, but no ulnar condyle, and in having a narrow intertubercular groove. Among fossorial therians humeral torsion occurs only in Chrysochloridae. The Spalacidae, which are fossorial, have no radial condyle, only a trochlea, as their forelimbs work in a parasagittal plane.

The small degree of humeral torsion (15°) found in one multituberculate taxon (*Bulganbaatar*) does not imply a parasagittal posture (as proposed by Sereno &

McKenna 1995), as lack of torsion occurs also in forms with sprawling posture such as the Anura, and in several digging therians, with secondarily abduct their forelimbs. *Bulganbaatar* has no trochlea, but has prominent radial and ulnar condyles, characteristic of forms with primary abducted forelimbs. Multituberculate humeri vary in the degree of torsion. It cannot be excluded that the relatively notable torsion of *Lambdopsalis* (24–38°) is, at least in part, related to its semi-fossorial mode of life. However, the structure of the multituberculate humerus, with spherical humeral head, wide intertubercular groove, lesser trochanter wider than the greater one, spherical radial condyle and prominent ulnar condyle, indicates a primary sprawling stance of the forelimbs.

The structure of the multituberculate scapula which is narrow and has convex medial side (subscapular fossa) indicates that the scapula was more movable than in any therian mammal. The rotation at the shoulder joint was ensured by both the rotation of the scapula and the rotation of the humerus. The structure of the multituberculate elbow joint, with spherical radial and ulnar condyles and very extensive articular circumference on the proximal end of the radius (Kielan-Jaworowska & Gambaryan 1994: fig. 16A), indicates a possibility of extensive rotation of the antebrachium and independent rotation of the radius about its longitudinal axis, as characteristic of abducted limbs. In several therians, e.g., scansorial forms, the radius also rotates about its longitudinal axis, but there is no rotation of both bones of the antebrachium together.

Kielan-Jaworowska & Gambaryan (1994) concluded on the basis of an analysis of multituberculate hind limbs, and structure of lumbar vertebrae with long transverse and high spinous processes, that multituberculates had sprawling limb posture and were adapted for asymmetrical gaits with steep jumps. In the present paper, we show that the range of humeral excursion at flexion-extension in the shoulder joint in multituberculates was much smaller than in *Didelphis*, and that during the swing phase the forelimbs were stretched anteroventrally, as characteristic of mammals before landing. This questions the hypothesis of Sereno & McKenna (1995) on *Didelphis*-like locomotion of multituberculates, and gives support to the supposition of Kielan-Jaworowska & Gambaryan (1994) that multituberculates were adapted for asymmetrical jumps with abducted limbs. At the beginning of the propulsive phase, just after landing, the humerus was oriented more sagittally than in the successive stages. Between the beginning and middle of the propulsive phase the body was falling down between the limbs, while the humeral head was depressed and the elbow joint flexed. Between the middle and the end of the propulsive phase the body elevated between the forelimbs, but not as high as at the beginning and the humerus was more abducted than at the beginning.

The fact that multituberculates never developed a trochlea and retained the condylar structure of the elbow joint throughout their history, while the ancestors of therians acquired the trochlea possibly during the Late Jurassic and very early lost the ulnar condyle, indicates that parasagittal posture arose in mammalian evolution only in therians, and not in common ancestors of therians and multituberculates. Although multituberculates and therians share many characters which may indicate close relationship (e.g., pattern of cranial vasculature and structure of ear ossicles), reconstruction of multituberculate stance and movements does not support multituberculate-therian sister-group relationship.

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Odwiedzione czy przystrzałkowe ustawienie kończyn multituberkulatów

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Streszczenie

Celem pracy było przetestowanie dwóch hipotez dotyczących położenia kończyn i sposobu poruszania się wymarłej grupy ssaków – multituberkulatów (wieloguzkowców). Kielan-Jaworowska & Gambaryan (1994) opisali dobrze zachowane szkielety multituberkulatów z osadów późnokredowych Mongolii, zrekonstruowali ich umięśnienie i wyciągnęli wniosek, że kończyny multituberkulatów były skierowane na boki (odwiedzione), tak jak u współczesnych gadów i stekowców. Wniosek ten opierał się głównie na analizie budowy kończyn tylnych, w których poprzeczna oś kości piszczelowej jest dłuższa niż podłużna, tak jak u czworonogów o kończynach odwiedzionych, gdy w przypadku kończyn parasagitalnych, dłuższa jest oś podłużna. Drugim argumentem było skierowanie osi stopy nie równolegle do płaszczyzny podłużnej ciała i osi kości piętowej, lecz odwiedzenie jej o 30° od osi kości piętowej, gdy u ssaków o kończynach parasagitalnych oś stopy leży w przedłużeniu osi kości piętowej. Długie wyrostki ościste i poprzeczne kręgów lędźwiowych wskazywały na przystosowanie multituberkulatów do poruszania się asymetrycznymi skokami. Kompletne kości ramienne zachowane u paleoceńskiego multituberkulata z Chin wykazywały skręcenie proksymalnych i dystalnych odcinków w stosunku do siebie, jak u większości czworonogów o odwiedzionych kończynach.

Sereno & McKenna (1995) opisali kość ramienną i część szkieletu barkowego multituberkulata z późnej kredy Mongolii. Kość ta nie wykazuje skręcenia, charakterystycznego dla stekowców i współczesnych gadów, w związku z czym autorzy wyciągnęli wniosek, że multituberkulaty miały kończyny parasagitalne (ustawione przystrzałkowo), tak jak współczesne ssaki właściwe, poruszały się podobnie jak oposy, oraz że parasagitalność powstała w ewolucji ssaków tylko raz u wspólnych przodków multituberkulatów i ssaków właściwych.

W pracy niniejszej przetestowano obie hipotezy w oparciu o porównania anatomiczne oraz rekonstrukcję ruchów kończyn przednich multituberkulatów. Wykazano że brak skręcenia kości ramiennej nie świadczy o parasagitalności, ponieważ nie skręcona kość ramienna występuje również u form z odwiedzionymi kończynami, np. u żab, oraz u licznych grzebiących ssaków łożyskowych, u których nastąpiło wtórne odwiedzenie kończyn. Porównując budowę stawu barkowego, kości ramiennej i stawu łokciowego czworonogów lądowych, ustalono listę cech kości ramiennej, które występują u czworonogów o pierwotnie odwiedzionych kończynach i wykazano że wszystkie te cechy występują u multituberkulatów, Są to: brak bloczka na kości ramiennej i obecność wypukłych kłykci promieniowego i łokciowego, szeroka bruzda międzyguzkowa, oraz guzek mniejszy kości ramiennej szerszy niż guzek większy. Przeprowadzono też rekonstrukcję ruchów kończyn przednich multituberkulatów i wykazano, że zakres ruchów zginania i prostowania w stawie barkowym był mniejszy niż u oposa, natomiast kość ramienna mogła bardziej niż u oposa wyciągać się ku przodowi i w dół, tak jak to występuje u ssaków podczas skoków. Odrzucono więc przypuszczenie Sereno i McKenny, że multituberkulaty poruszały się podobnie jak współczene oposy. Wyciągnięto wniosek ze budowa kończyn przednich (tak jak i tylnych) multituberkulatów wskazuje na odwiedzione położenie kończyn i udział skoków w ich lokomocji. Brak nawet zaczątkowego bloczka na kości ramiennej u wszystkich znanych multituberkulatów wskazuje, że nie powstała u nich parasagitalność. Parasagitalność w ewolucji ssaków powstała tylko u ssaków właściwych (Theria). Chociaż multituberkulaty i ssaki właściwe wykazują wiele cech wskazujących na ich pokrewieństwo (np. przebieg naczyń krwionośnych głowy, budowa kostek słuchowych itd.), położenie ich kończyn nie potwierdza hipotezy, że są to grupy siostrzane.