

Postcranial anatomy of *Haldanodon expectatus* (Mammalia, Docodonta) from the Late Jurassic (Kimmeridgian) of Portugal and its bearing for mammalian evolution

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The postcranium of the Late Jurassic docodont *Haldanodon expectatus* Kühne & Krusat, 1972 is represented by a partial skeleton and isolated bones of other individuals from the Late Jurassic (Kimmeridgian) of the Guimarota coal mine in Portugal. *Haldanodon* exhibits adaptations for a fossorial lifestyle such as stout and short limb bones and humeri with greatly expanded distal joints and strong deltopectoral crests. Short first and second phalanges and moderately curved and laterally compressed terminal phalanges with lateral grooves suggest that *Haldanodon* was a scratch-digger. The dorso-ventrally elongated, triangular scapula has a convex transverse profile with strongly laterally reflected anterior and posterior scapula margins, enclosing a deep trough-like ‘infraspinous fossa’. A supraspinous fossa is not developed. The saddle-shaped glenoid facet is mainly formed by the coracoid and orientated antero-ventrally indicating a sprawling gait. No epiphyses were detected and the wide size range of humerus and femur possibly indicate a lifelong growth. *Haldanodon* is more derived than *Morganucodon* by complete reduction of the procoracoid, absence of the procoracoid foramen, and a peg-like coracoid. It shares with monotremes a postscapular fossa that is absent in *Morganucodon*. A PAUP analysis based on 280 cranio-dental and postcranial characters corroborated the position of *Haldanodon* above morganucodontids and below *Hadrocodium*. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 145, 219–248.

ADDITIONAL KEYWORDS: fossorial – Guimarota – limb posture – Mesozoic mammals – phylogeny – postcranium.

INTRODUCTION

Fieldwork in the Guimarota coal mine near Leiria, Portugal by the Institut für Paläontologie of the Freie Universität Berlin yielded about two dozen skulls and more than 800 dentaries of multituberculates, holotherians, and docodonts (Martin & Krebs, 2000). During the systematic excavation from 1973 to 1982 (new excavations) two more or less complete mammalian skeletons were found, of which one is that of the paurodont *Henkelotherium guimarotae* Krebs, 1991 discovered in 1976 (Henkel & Krebs, 1977; Krebs, 1991, 2000). The second partial skeleton with skull and lower jaw associated was found in 1979 and belongs to the only docodont taxon known from the

Guimarota locality, *Haldanodon expectatus* Kühne & Krusat, 1972. Short reports on this skeleton have been given by Henkel & Krusat (1980) and by Krusat (1991), and a life-reconstruction has been figured and shortly discussed by Martin & Nowotny (2000). However, in contrast to the dentition (Krusat, 1980) and particularly the cranio-mandibular morphology (Lillegraven & Krusat, 1991), the postcranial anatomy of *Haldanodon* has never been described and analysed in detail.

Haldanodon is only the second Jurassic mammal of which large parts of the postcranial skeleton have been found in association with the skull. The *Haldanodon* skeleton was found in a single fist-sized piece of lignite, with the skull and most of the associated (albeit disarticulated) postcranial bones visible at the surface. During preparation it was decided not to sep-

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arate the disarticulated bones belonging to the skeleton but to conserve them in their original position (Henkel & Krusat, 1980). For this purpose the transfer method described by Kühne (1961, 1962), previously proven to be effective during the preparation of the *Henkelotherium* skeleton, was used to prepare the *Haldanodon* skeletal specimen (Drescher, 1989, 2000). After the bones had been freed from the matrix on one side a transparent polyester resin was poured on the specimen. After polymerization, the slab containing the fossil was turned upside down and the remaining rock matrix was completely removed. The bones are now fixed in their original position by the resin matrix. Grinding and polishing of the bottom of the transparent plastic block also allows examination of the bones on the side which is now covered by the resin. Some of the postcranial bones belonging to the skeleton have been separated and are now kept isolated, because they had been embedded in different bedding planes within the coal. With exception of a few ribs, no parts of the axial skeleton and none of the pelvis are preserved.

Among the isolated postcranial bones from the Guimarota collection about 25 specimens have been identified as belonging to *Haldanodon exspectatus*. Those bones have been completely freed from the matrix and can be studied from all aspects.

MATERIAL AND METHODS

The *Haldanodon* specimens described here are currently housed at the Institut für Geologische Wissenschaften, Fachrichtung Paläontologie of the Freie Universität Berlin (IPFUB) under the collection numbers given (Gui, Guimarota; Mam, Mammalia, plus subsequent number/year of collection; e.g. Gui Mam 47/75 means specimen number 47, collected in 1975). In specimens with single numbers (e.g. Gui Mam 3003), the date of collection is given in parentheses (day.month.year). The specimens available for study and measurements are listed in Table 1. AG, Alte Grabung [old excavation] from 1959 to 1961; NG, Neue Grabung [new excavation] from 1973 to 1982; OS, osteological collection of IPFUB; ZMB, Museum für Naturkunde der Humboldt-Universität zu Berlin, zoological collection; An, Museum für Naturkunde der Humboldt-Universität zu Berlin, anatomical collection; CM, Carnegie Museum of Natural History, Pittsburgh, PA (USA); NGMC, National Geological Museum of China, Beijing. All measurements are given in millimetres (mm).

PARTIAL SKELETON OF *HALDANODON EXSPECTATUS*

Gui Mam 30/79, incomplete skeleton with skull (anterior portion isolated), right (partially isolated)

and left (isolated) scapulo-coracoid, right and left (isolated) humerus, right and left (isolated) ulna, right radius, left femur, right tibia, three phalanges (two on the plastic slab, one isolated which before was sitting between ulna and femur), and two isolated ribs and three isolated rib fragments. Henkel & Krusat (1980: 215) mention isolated carpals, respectively, tarsals without further description; among the material attributed to Gui Mam 30/79 no isolated carpals or tarsals were found by the author.

ISOLATED BONES DERIVING FROM OTHER INDIVIDUALS

Pectoral girdle: Gui Mam 3000 (NG 14.5.82), left scapulocoracoid; Gui Mam 3008 (NG 6.5.76), right scapulocoracoid. Forelimb: Gui Mam 3001 (AG 9.9.61), left humerus; Gui Mam 3002 (NG 17.12.73), left humerus; Gui Mam 3003 (NG 23.9.74), right humerus fragment (sectioned for histological analysis); Gui Mam 3007 (NG 29.3.75), left humerus; Gui Mam 3009 (NG 5.8.77), left humerus, deltopectoral crest broken off; Gui Mam 3010 (NG 21.4.82), right humerus; Gui Mam 3004 (NG 14.12.73), right ulna; Gui Mam 94/74, right ulna. Pelvic girdle: Gui Mam 3011 (NG 18.8.76), left ilium. Hindlimb: Gui Mam 47/75, right femur. Phalanges: Gui Mam 3006 (AG without collection date): metapodial; Gui Mam 132/74, two small unidentified carpals or tarsals, two metapodials, one phalanx I, five phalanges II, two terminal phalanges associated with toothed maxilla.

MATERIAL USED FOR COMPARISONS

Trechnotheria: *Zhangheotherium quinquecuspidens*, NGMC 352, incomplete skeleton, Early Cretaceous, Yixian Formation, Liaoning, China. Monotremata: *Ornithorhynchus anatinus*, IPFUB OS without number, skeleton, no data; CM 1788, skeleton, locality unknown. *Tachyglossus aculeatus*, IPFUB OS without number, skeleton, zoo specimen; IPFUB OS La 670, mounted skeleton, no data; CM 1787, skeleton, Tasmania. Placentalia: *Manis javanica*, IPFUB OS 11, skeleton, Indonesia, coll. Dr. Kern 1971. *Tatusia novemcincta*, CM 1710, skeleton, Sta. Catharina, Brazil. *Talpa europaea*, IPFUB OS 2, skeleton, Spremlingen near Frankfurt (Hesse, Germany); IPFUB OS without number, skeleton, Berlin 1953. *Galemys pyrenaicus*, ZMB 14659, skeleton, no data. *Desmana moschata*, ZMB 33829, skeleton, Sarepta (Russian Federation). *Calcichloris obtusirostris*, ZMB 35173, skeleton, South Africa 1927. *Chrysochloris capensis*, An 3857, skeleton, Cap. *Amblysomus hottentotus*, CM 94943, skeleton, South Africa, Cape Province. *Eremitalpa granti namibiensis*, CM 93155, skeleton, South-west Africa, Namib Desert.

Table 1. Measurements (in mm) of bones of the appendicular skeleton of *Haldanodon expectatus*

Specimen/Measurement							
SCAPULOCORACOID							
Specimen no.	30/79 (l)	30/79 (r)	3000	3008			
Height (dorsoventral)	16.0	–	22.7	(21)			
Glenoid facet length	3.7	3.7	5.0	4.2			
Glenoid facet width	2.5	2.5	3.8	3.3			
HUMERUS							
Specimen no.	30/79 (l)	30/79 (r)	3001	3009	3010	3007	3002
Length	11.9	11.8	(12)	14.0	(18)	(18.5)	–
Proximal width	5.1	–	(5)	(6)	–	–	–
Distal width	7.3	(7)	8.2	8.6	(10)	10.3	–
Sm. diam. shaft	2.5	2.3	2.5	3.0	3.5	3.6	3.7
RADIUS							
Specimen no.	30/79 (r)						
Length	10.1						
Proximal width	2.0						
Distal width	2.5						
ULNA							
Specimen no.	30/79 (r)						
Length	14.0						
Olecranon length (above pivot of semilunar notch)	3.8						
ILIUM							
Specimen no.	3011 (l)						
Length	(14)						
Height	5.1						
Width	3.4						
FEMUR							
Specimen no.	30/79 (l)	47/75 (r)					
Length	14.4	20.0					
Width between trochanters	6.3	9.7					
Width of distal joint	4.3	7.7					
TIBIA							
Specimen no.	30/79 (r)						
Length	11.6						
Smallest diam. of shaft	1.7						
Proximal width	4.1						
Distal width	2.1						
METAPODIAL							
Specimen no.	132/74–7	132/74–8	3012				
Length	3.9	3.0	3.3				
Width	(2.3)	1.8	1.5				
PHALANX I							
Specimen no.	132/74–6						
Length	2.2						
Width	1.9						
PHALANX II							
Specimen no.	30/79	132/74–1	132/74–2	132/74–3	132/74–4	132/74–5	
Length	2.2	2.7	2.5	2.8	2.6	2.9	
Width	1.6	2.3	2.0	2.3	1.6	1.8	
TERMINAL PHALANX							
Specimen no.	132/74–10	132/74–9					
Length	4.2	3.0					
Width	1.2	1.2					

Estimates are in parentheses. diam, diameter; l, left, r, right; sm, small.

DESCRIPTION

SKULL

The skull is visible in a ventral aspect with the posterior portion preserved on the main slab. The left premaxillary has the alveoli for I1–5. Both maxillary bones have teeth, and the anterior part of the right ramus with i3–5, c, p1–3, and m1 are preserved separately. The left maxillary holds the alveolus for I4, canine, alveolus for P1, P2–3, M1–3; in the right maxillary the incisor, alveolus for P1, P2–3 and M1–3 are preserved. The coronoid process and part of the ramus with last and penultimate molars of the right mandible are partially embedded in the plastic. The right M5 has fallen out and is preserved on the main slab. The left jugal is displaced and embedded between the tibia and right scapula fragment. The morphology of the teeth unambiguously indicates that the skeleton belongs to *Haldanodon expectatus*, the only docodont species present in the Guimarota locality. Of the skull bones, the right squamosal can be clearly identified (Fig. 1); the other skull bones are very broken on the ventral side. In a dorsal aspect, through the transparent plastic, flat frontal and parietal bones are visible. A detailed description of the skull anatomy of *Haldanodon expectatus* has been given by Lillegraven & Kruusat (1991) and does not need to be repeated here.

AXIAL SKELETON

Ribs: No vertebrae are preserved from the axial skeleton of Gui Mam 30/79. The only axial skeletal parts which have been found in association with the skeleton are two nearly complete ribs and three rib fragments. In the most complete specimen (Fig. 2), most probably a left middle thoracic rib, only a small part of the distal end is missing. The rib is double-headed with the tubercle sitting dorsally of the head; their articulation facets are very closely positioned and are only separated by a narrow constriction. In its proximal third the shaft is curved and has an oval cross section; more distally, the shaft is flattened anteroposteriorly and is straight; therefore a rather deep thorax can be inferred. The *Haldanodon* rib is comparable in size to the ribs of *Talpa europaea*. The second thoracic rib (also from a middle position) is probably from the right side; it is somewhat damaged at the proximal end and both heads and the distal parts are missing. Morphologically, it closely resembles the more complete specimen. The third thoracic rib from the anterior or middle region is a proximal fragment (about one third) with slightly damaged proximal end and only the tubercle preserved. The other two rib fragments are more flattened. One of the fragments with broken proximal end has a blade-like shape and

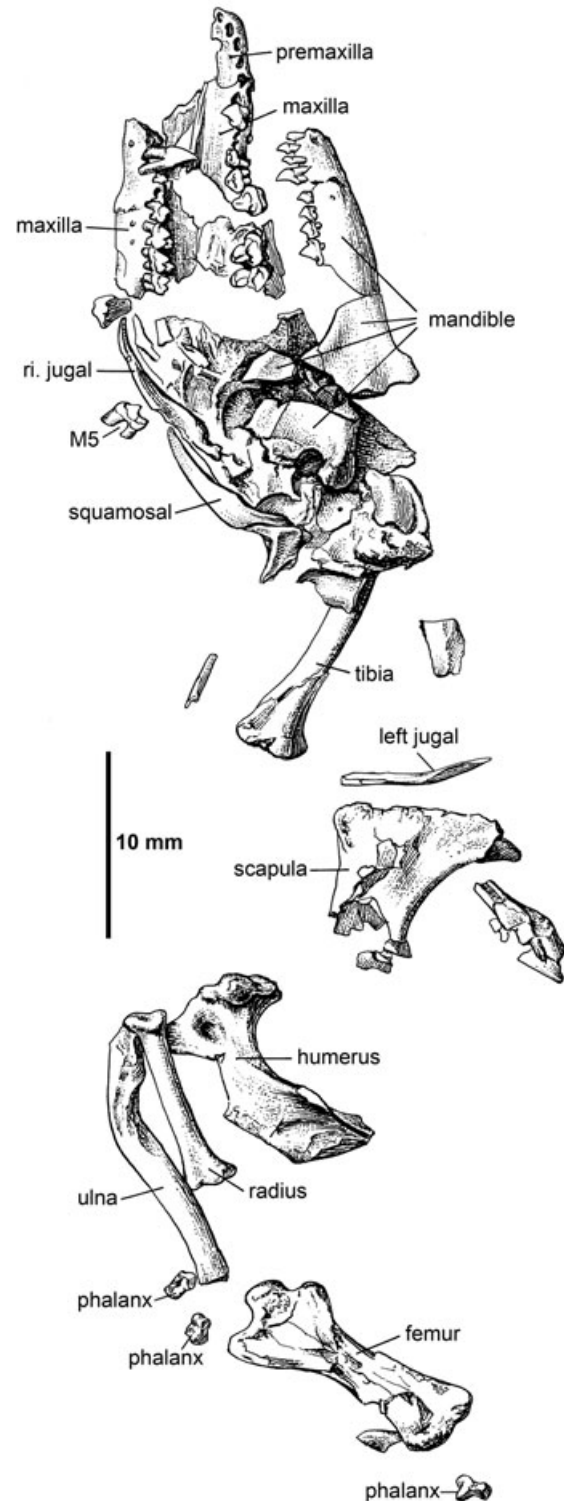


Figure 1. *Haldanodon expectatus*, Gui Mam 30/79. Incomplete and dislocated postcranial skeleton associated with skull and right mandible. M5, fifth upper molar; ri, right.

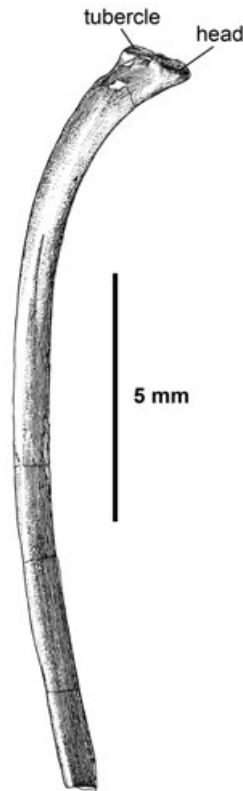


Figure 2. *Haldanodon exspectatus*, Gui Mam 30/79. Left thoracal rib in a caudal aspect (posterior view).

differs considerably from the thoracal ribs; the undamaged distal end has a rugose surface. The other specimen is broken at the proximal and distal end. These flat rib fragments can be interpreted as sternal ribs, and the more flattened specimen most probably comes from a more posterior position.

PECTORAL GIRDLE

Scapulocoracoid: Four scapulocoracoids were available for study: the left and right scapulocoracoid of the skeleton (Gui Mam 30/79; Fig. 3) and two isolated, much larger specimens (Gui Mam 3000 and 3008; Figs 4, 5). The right scapulocoracoid of the skeleton is broken and incomplete. Its scapular part is preserved on the plastic, and its coracoidal part has been separated and is preserved isolated. The left scapulocoracoid of Gui Mam 30/79 is completely isolated; it is well preserved at the posterior side while the anterior part of the scapula is broken. Gui Mam 3000 is a very large specimen with largely complete coracoidal part and somewhat damaged scapula. In Gui Mam 3008 the scapula is better preserved.

The scapulocoracoid of *Haldanodon* (Fig. 6) is a large bone, consisting of the scapula and the coracoid

which are fused by a suture in the wide glenoid cavity (visible in the left scapulocoracoid of Gui Mam 30/79). The scapula has an acute triangular shape with the tip pointing ventrally. The anterior margin is straight, and the posterior margin is concave. The dorsal border is gently convex with a rugose edge which indicates the former presence of a cartilaginous part. The dorsal margin of the scapula forms a hook-like process pointing posteriorly.

The cranial (anterior) margin of the scapula is more or less broken in all specimens. In Gui Mam 3000 its dorsal part is preserved as a plastic cast of the natural mould in the coal. In Gui Mam 3008 large parts of the anterior margin are present, although they were somewhat displaced and appressed to the scapula blade during fossilization. From the preserved remains it is clear that the anterior margin of the scapula was strongly laterally recurved. Traditionally, the anterior scapula margin of nontherians is considered to be homologous to the scapular spine of therian mammals (Romer, 1922; Jenkins & Weijs, 1979), a view that has been contested by Sánchez-Villagra & Maier (2002, 2003) on the basis of ontogenetic studies in marsupials. According to Sánchez-Villagra & Maier (2002, 2003), the portion of the therian scapular spine that is situated dorsal to the acromial process represents a neomorphic structure. In nontherian mammals, only the portion that is located at the origin of the acromial process is homologous to the therian scapular spine. There is no trace of a supraspinous fossa cranially of the recurved anterior margin of the *Haldanodon* scapula.

The posterior (= caudal) edge of the scapula (almost completely preserved in Gui Mam 3008) is strongly recurved laterally. Dorsally, it continues as a spine-like crest and separates the postscapular fossa and its hook-like posterior extension from the main part of the scapula. Ventrally, it runs slightly anteriorly and fades before reaching the dorsal rim of the glenoid facet. Anterior and posterior recurved margins enclose a very deep trough-like 'infraspinous fossa', that morphologically differs from the flat and posteriorly open infraspinous fossa of therian mammals. The deep trough-like 'infraspinous fossa' of *Haldanodon* indicates a strong shoulder musculature. According to Sánchez-Villagra & Maier (2002, 2003), only the ventral portion of that fossa is homologous to the therian infraspinous fossa. Due to the laterally reflected anterior and posterior margins the transverse profile of the scapula is convex.

The acromion is preserved in the right scapulocoracoid of the skeleton (Gui Mam 30/79) and it forms the ventralmost part of the reflected anterior scapular margin. It is flattened medio-laterally and forms a short process that does not extend beyond the dorsal margin of the glenoid facet. A comparatively large oval

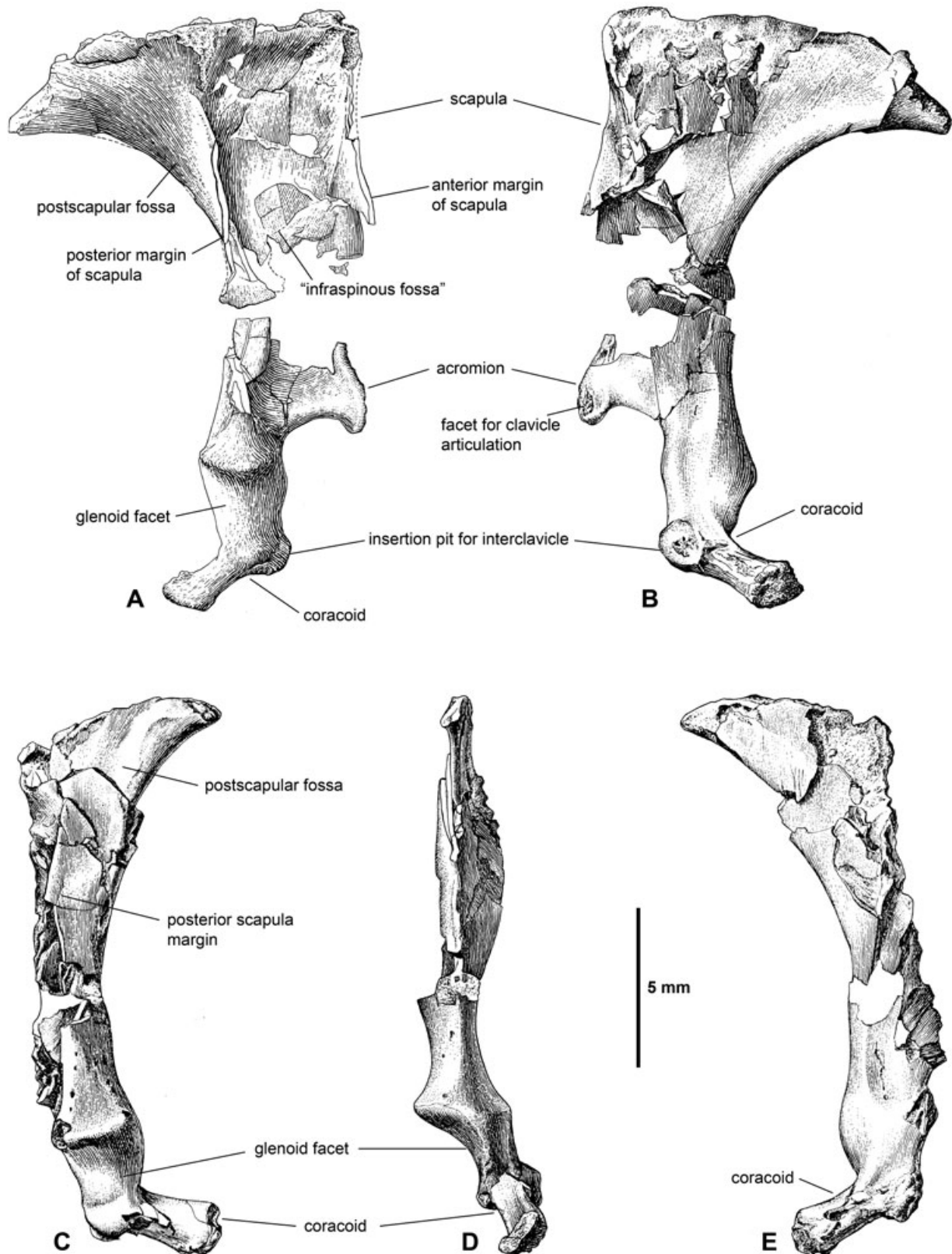


Figure 3. *Haldanodon exspectatus*, Gui Mam 30/79. A and B, right scapulocoracoid in: A, lateral and B, medial views. C–E, left scapulocoracoid in: C, lateral; D, caudal and E, medial views.

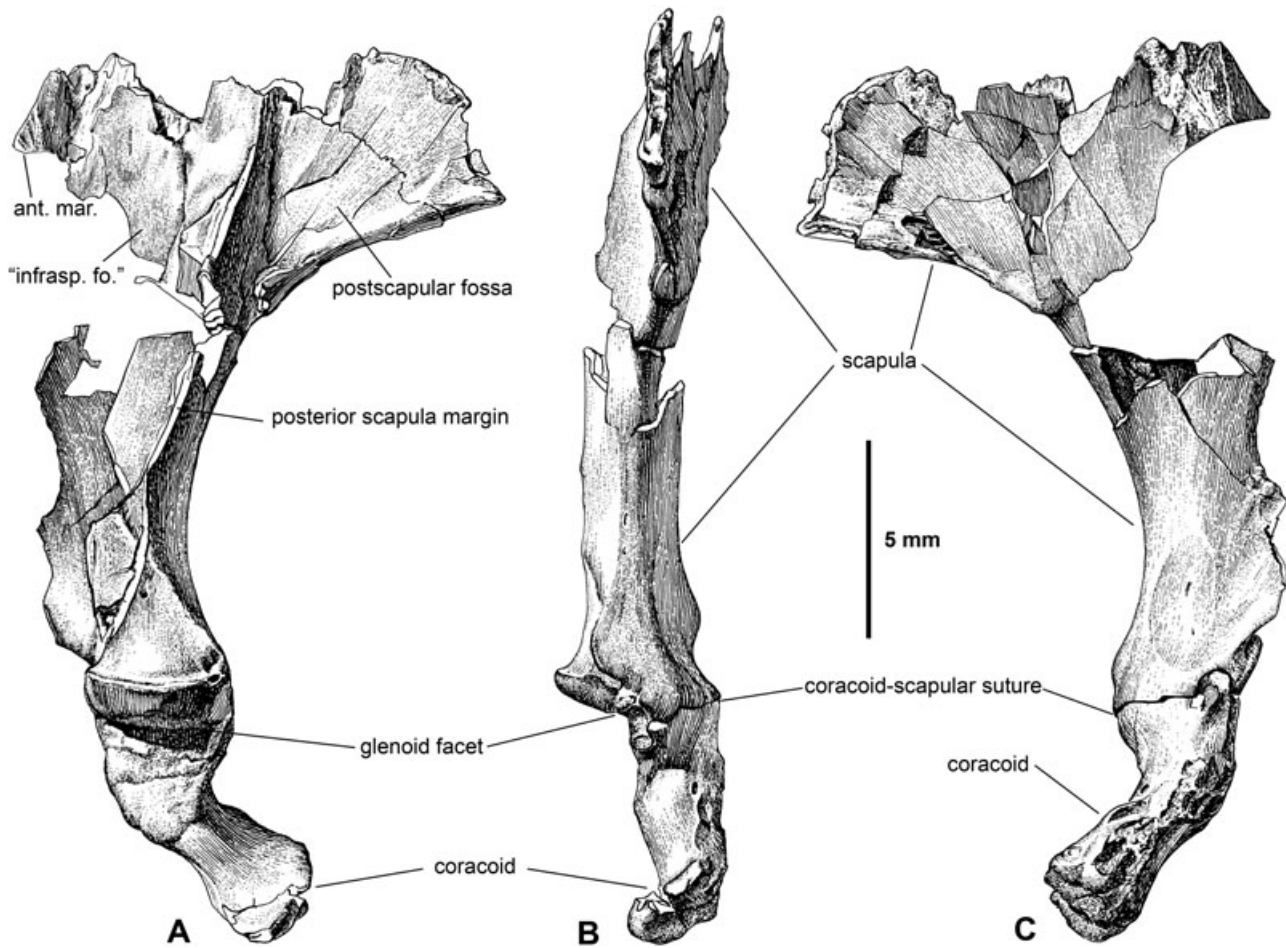


Figure 4. *Haldanodon expectatus*, Gui Mam 3000. Left scapulocoracoid in: A, lateral; B, caudal and C, medial views. ant. mar., anterior margin; 'infrasp. fo.', 'infraspinous fossa'.

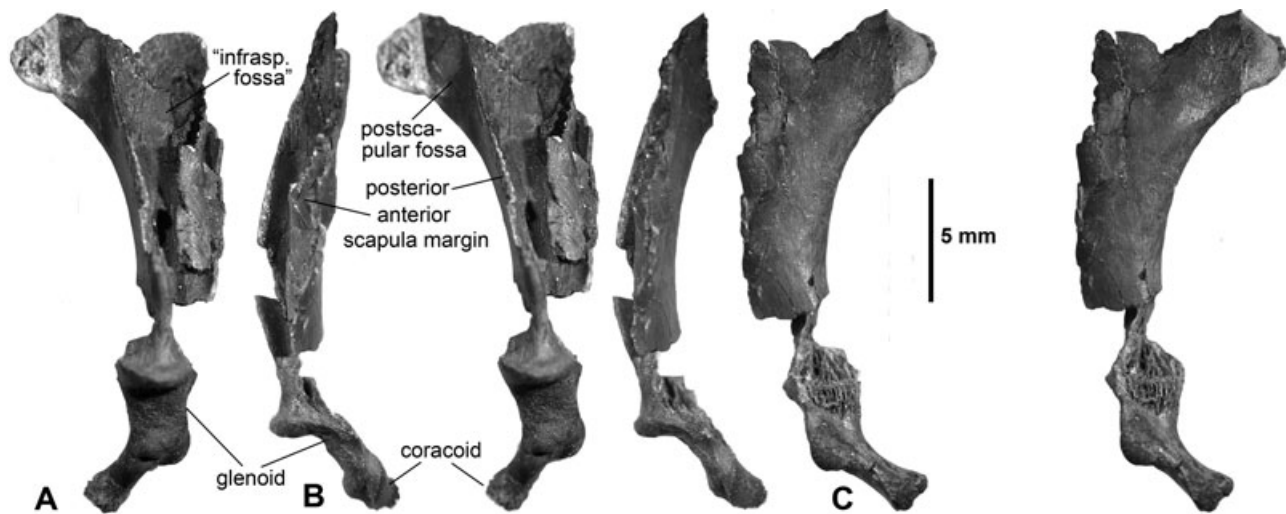


Figure 5. *Haldanodon expectatus*, Gui Mam 3008. Right scapulocoracoid in: A, lateral; B, anterior and C, medial views (stereo-pairs). infrasp., infraspinous.

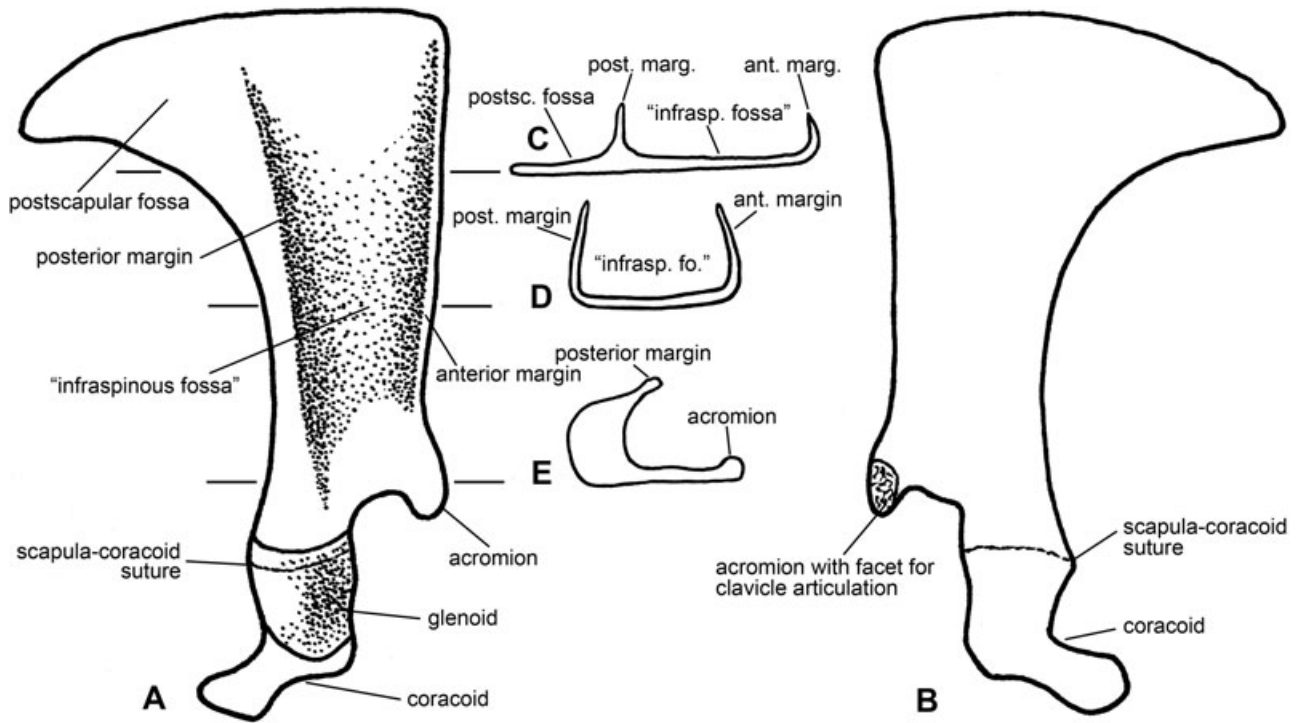


Figure 6. Reconstruction of the right scapulocoracoid of *Haldanodon expectatus* based on specimens Gui Mam 30/79, Gui Mam 3000, and Gui Mam 3008. A, lateral view; B, medial view; C–E, cross sections of scapula with section planes marked. Suture between scapula and coracoid in dorsal part of glenoid. ant., anterior; infrasp., infraspinous; marg., margin; post., posterior; postsc., postscapular.

area with slightly rugose surface on the medial side of the acromion represents the facet for the clavicle. The contact surface of the acromion for the clavicle clearly shows the two bones had a rigid articulation, as in extant monotremes.

The broadly curved glenoid is formed mainly by the coracoid and only at two fifths of its length by the ventromedial part of the scapula. The suture between both bones is well fused in all specimens and can be best seen in the left scapulocoracoid of Gui Mam 30/79. The glenoid facet is oval and saddle-shaped; it narrows slightly in ventral direction. Orientation of the glenoid facet is latero-ventrally.

The coracoid is a peg-like structure; at its tip it bears a tuberosity for attachment for the coracoid head of the triceps as observed in cynodonts and monotremes (Jenkins & Parrington, 1976: 399). A coracoid groove (Serenó & McKenna, 1995: fig. 8a) is not developed. A procoracoid was not detected, this bone apparently had been already reduced in *Haldanodon*; consequently the procoracoid foramen is absent.

A rugose area on the ventromedial side of the apex of the coracoid probably marks the insertion place for the manubrium sterni and/or the interclavicle, although the interclavicle itself is not preserved.

FORELIMB

Humerus: The humerus of Gui Mam 30/79 (Figs 7–8) is short and robust and is even stronger and thicker than the femur of the same individual. It has a very large, wing-like deltopectoral crest which extends antero-medially, indicating a strong deltoid muscle. The deltopectoral crest originates at the antero-lateral side of the caput humeri and is confluent with the comparatively small greater tubercle. It ceases abruptly at the midshaft and does not extend beyond that point. In its distal portion, the anterior edge of the deltopectoral crest is somewhat flattened and bears an area with rugose bone structure for tendon attachment. The lesser tubercle on the medial side of the humerus head is much larger than the greater tubercle; it is wing-shaped and bent posteriorly. In the midshaft of the humerus and somewhat extending beyond that point, a large teres tuberosity with rugose muscle attachment mark is developed; it is separated from the lesser tubercle by a shallow depression. Greater tubercle/deltopectoral crest and lesser tubercle/teres tuberosity are separated by a shallow and wide intertubercular groove, that extends until the midshaft. The shaft of the humerus is broad with a flat dorsal (posterior) side.

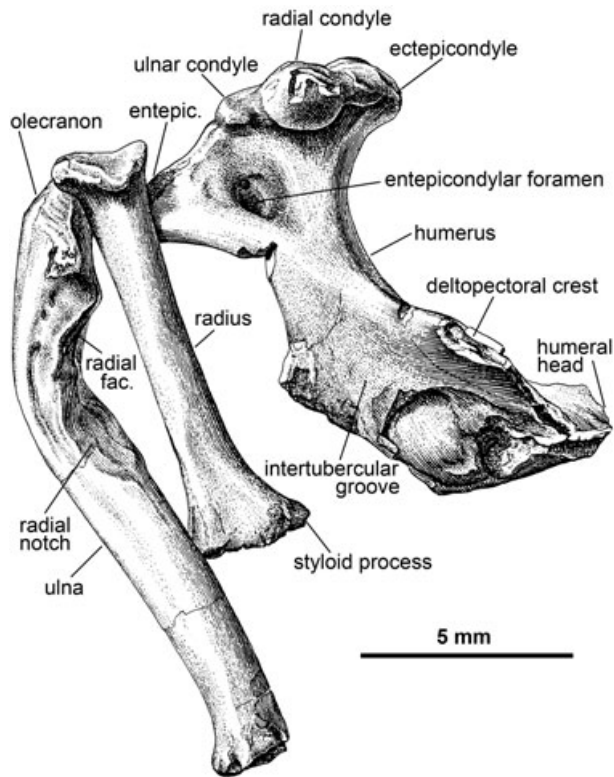


Figure 7. *Haldanodon expectatus*, Gui Mam 30/79. Right forelimb as originally preserved, with (from right to left) humerus in anterior view (distal end pointing upwards), radius in an anterior view, and ulna in a lateral aspect. entepic., entepicondyle; fac., facet.

The shoulder and elbow joints are very broad and twisted to each other at an angle of about 60°, giving the bone a waisted hourglass shape. The head of the right humerus of Gui Mam 30/79 is covered by an artificial matrix but can be studied through the transparent plastic. The left humerus is preserved isolated and can be examined from all aspects. The head is broad and cylindrical with a notch-like extension at the lateral side which is somewhat damaged in the left humerus. The distal end is also strong and very broad (distal width is 61.3% of humeral length; 61.4% in Gui Mam 3009). No trochlea is developed. The large radial condyle is spherical with a cylindrical lateral extension which ends in a small ectepicondyle with rugose bone surface for tendon attachment of the forearm extensor muscles. The ectepicondyle leads to a well-developed supinator process with a rugose area for tendon attachment. The medial ulnar condyle is bulbous and somewhat compressed mediolaterally; it is considerably smaller than the radial condyle. Both condyles are separated by a notch. On the medial side, a large and robust entepicondyle with a well-developed muscle or tendon attachment area is present; the

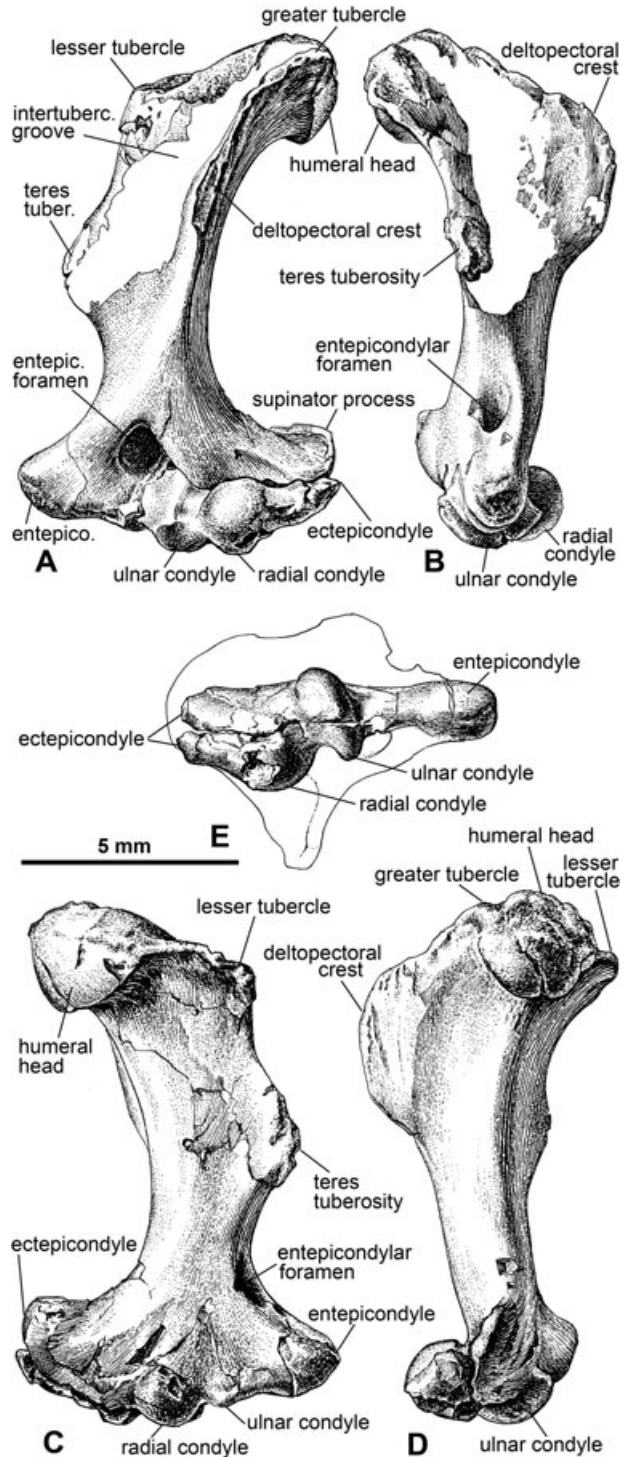


Figure 8. *Haldanodon expectatus*, Gui Mam 30/79. Left humerus in: A, anterior; B, medial; C, posterior; D, lateral; and E, distal view. entepic., entepicondylar; entepico., entepicondyle; intertuberc., intertubercular; tuber., tuberosity.

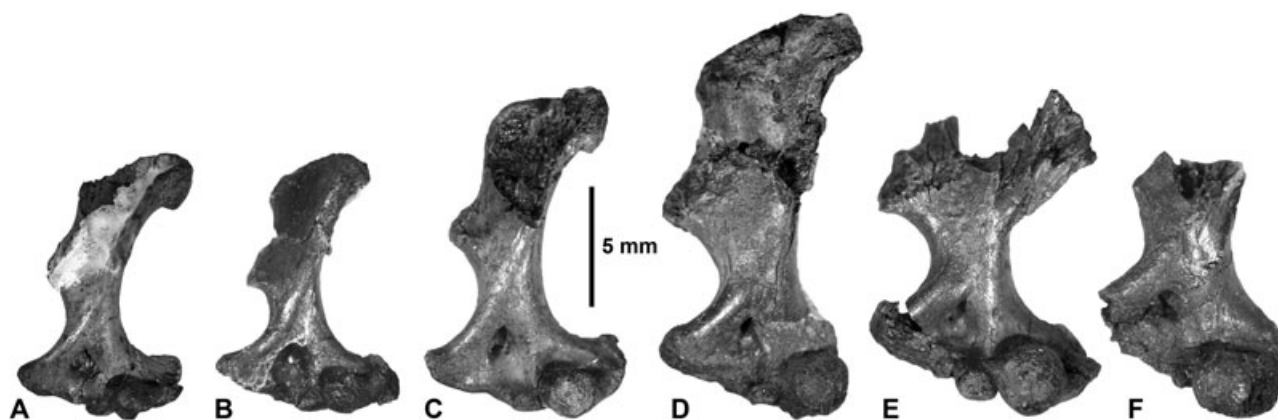


Figure 9. *Haldanodon expectatus*, growth series of left humeri in anterior view. A, Gui Mam 30/79; B, Gui Mam 3001, proximal head partially missing; C, Gui Mam 3009; D, Gui Mam 3010 (reverted), proximal head partially missing; E, Gui Mam 3007, proximal part of shaft and head missing; F, Gui Mam 3002, distal portion of humerus.

entepicondyle is separated from the medial condyle by a broad shallow notch.

Above the distal joint, somewhat shifted medially, opens a large, drop-shaped entepicondylar foramen. It leads to the medial side of the humerus where it forms a somewhat smaller oval opening above the entepicondyle. The posterior side of the humerus is flat and an olecranon fossa is not developed.

Besides both humeri of specimen Gui Mam 30/79, six isolated and incomplete humeri of *Haldanodon* were available for study. All humeri morphologically closely resemble the humeri of Gui Mam 30/79, but the size variation is considerable (Fig. 9 and Table 1). Specimens Gui Mam 3001 and 3009 correspond in their dimensions to the humeri of the skeleton, but the other specimens are up to 1.5 times larger. Epiphyses were not detected in any of the humeri or other bones of *Haldanodon*. *Haldanodon* apparently had an extended, possibly lifelong, period of growth resulting in a very wide size range of its humeri and other postcranial elements. The well-preserved specimen Gui Mam 3007 has remarkably strong processes and muscle insertion marks indicating that it derives from an old individual.

Radius: Only the right radius of Gui Mam 30/79 was available for study (Fig. 7). It is exposed in an anterior aspect, the posterior side is hidden in the plastic. The radius is still in contact with the ulna but is not in articulation. It is shifted somewhat proximally, and the ulnar facet is in contact with the olecranon; therefore this facet cannot be examined. The radius is much shorter than the ulna (about 70% of the ulnar length) and is also shorter than the humerus. The stout shaft is straight and has an oval cross section. Its surface is smooth. The distal end is broader than the proximal. The articulation facet for the radial condyle at the

proximal end is bowl-like with a circular outline and is orientated somewhat obliquely to the shaft. On the lateral side of the distal third of the radius shaft the rugose flat contact plane for the ulna is visible. The distal end of the radius is broadened medio-laterally. There is a short and blunt styloid process present at the medial side of the distal end; it is slightly damaged medially. The distal articulation facet for the scapholunatum is a shallow bowl and is orientated transversely to the long axis of the radius.

Ulna: In the skeleton Gui Mam 30/79 the right ulna is almost complete and preserved in the artificial matrix (Fig. 7). Of the left ulna a proximal fragment with articulation facets and olecranon is preserved isolated. Two additional isolated fragmentary ulnae were available for study. Gui Mam 3004 is a right ulna with the proximal part of the tuber olecrani and the distal part of the ulnar shaft missing. This specimen is about twice as large as the ulna of the skeleton. Gui 94/74 is a right ulnar fragment with the proximal part of the olecranon and about one half of the shaft missing. This specimen is about 1.5 times larger than the ulna of the skeleton.

The right ulna of the skeleton Gui Mam 30/79 is preserved associated with the radius but not in articulation, because it was shifted distally postmortally; it is visible in a lateral aspect. The ulna is considerably longer than the radius which is mainly due to the large olecranon. The part of the ulna formed by the olecranon and the proximal articulation facets is about the same length as the shaft. The olecranon is inflated proximally and the olecranon tuber has a rugose surface for tendon insertion. An anconeal process is not developed and the coronoid process is very small. The proximal joint is long and exhibits two facets, one for the ulnar and one for the radial condyle of

the humerus, as well as the radial notch. In the right ulna of Gui Mam 30/79 the facet for the ulnar condyle of the humerus is hidden in the plastic, but it can be studied on the left ulna of the skeleton and other isolated specimens. Both articulation facets are shallow and are not clearly distinct from each other. The facet for the ulnar condyle of the humerus is not semicircular but much less curved and the facet for the radial condyle of the humerus is not bowl-like as in most therian mammals. The shallow radial notch is drop-shaped and proximo-distally elongated.

The large and bulbous olecranon is only slightly bent cranially. On the lateral and medial sides of the olecranon a groove runs parallel to the articulation facets. On the lateral side, the groove fades about midshaft while it runs down to the distal end on the medial side. The shaft is only moderately laterally compressed and has a rounded lateral and a flat-to-slightly-concave medial side (as visible through the transparent plastic). The interosseus border is rounded and only slightly rugose. The partially damaged distal articulation facet forms a shallow bowl. A small styloid process is present that does not extend beyond the distal facet.

Gui Mam 94/74 is a proximal fragment of a right ulna that was found in association with a mandible and two isolated teeth of *Haldanodon*. The isolated fragment as well as the left ulna of Gui Mam 30/79 allow examination of the medial side of the ulna which exhibits a well-developed groove along the long axis. In this ulnar fragment the medially situated shallow articulation facet for the ulnar condyle of the humerus is also clearly visible.

PELVIC GIRDLE

Ilium: Gui Mam 3011 is an isolated left ilium (Fig. 10). The bone is stout and robust, with a short body and a triangular cross section in the region

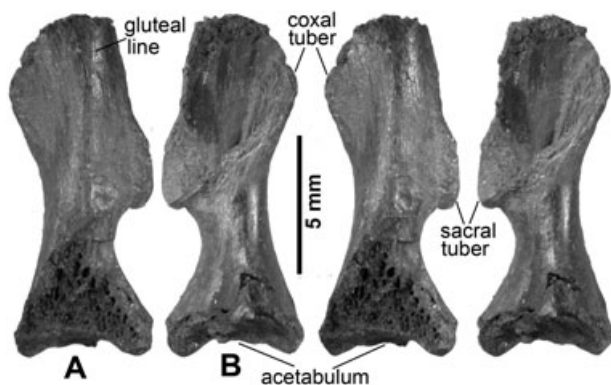


Figure 10. *Haldanodon expectatus*, Gui Mam 3011. Left ilium in: A, lateral and B, medial aspects (stereo-pairs).

between the ilio-sacral joint and the acetabulum. The anterior half of the ilium is broad and dorsally bears a strong sacral tuber that abruptly rises in the middle of the bone and gradually slopes in an anterior direction. The sacral tuber has a rugose surface for tendon and ligament insertion. On the lateral side a well-developed gluteal line is present that separates a dorsal narrow, flat to slightly convex area from a wider more concave ventral area. The anteriormost portion of the ilium is broken and apparently was bent laterally. Distal of the sacral tuber the lateral surface is damaged. The ventral border of the ilium is shallow concave and the coxal tuber is less prominent than the sacral tuber. At the distal end a segment of the comparatively large and shallow acetabulum is preserved. The medial side of the iliac shaft is flat. The sacral joint is very strong with a wider, medio-ventrally facing and a narrower, dorsally facing contact plane that both have a rugose and wrinkled surface. The articular surface extends over half of the preserved length of the ilium indicating a high number of sacral vertebrae.

HINDLIMB

Femur: In the skeleton Gui Mam 30/79 only the left femur is preserved in a posterior aspect (Fig. 11). The bone is almost complete, but has been crushed and

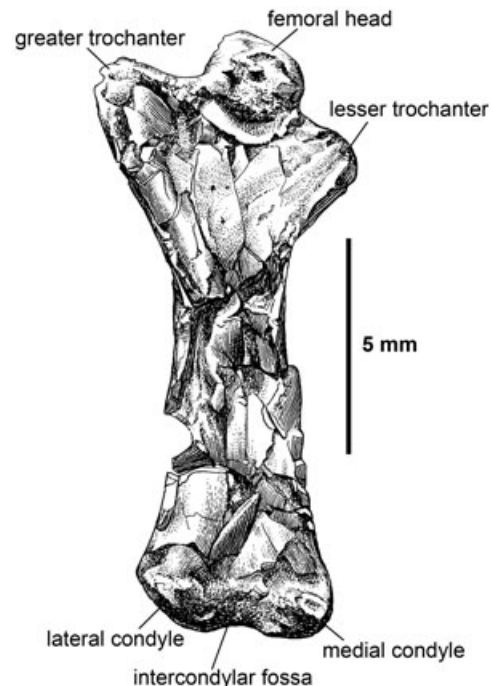


Figure 11. *Haldanodon expectatus*, Gui Mam 30/79. Left femur as originally embedded in a posterior (= ventral) aspect. The width of the shaft is exaggerated due to crushing during fossilization.

flattened by the sediment pressure. Like the humerus, the femur of *Haldanodon* is broad and robust. It has an hour-glass shape due to the strongly developed triangular trochanters and the broad distal joint. The shaft has an oval cross section and is comparatively short. It broadens precipitously towards the distal and proximal joints. Slightly proximally from the midshaft a nutritial foramen is located on the dorsolateral side. In a dorsal aspect, the large femoral head has a cylindrical shape and overlaps dorsally; on the ventral side, it is somewhat flattened. The head sits almost in the middle of the shaft and is only slightly shifted medially; a distinct collum is not developed. In a lateral aspect it becomes obvious that the head is not in alignment with the long axis of the femur but is slightly inclined dorsally. In the isolated femur Gui Mam 47/75 (Fig. 12) the head can be studied in all aspects; it does

not have a fovea for attachment of the femoral head ligament. The triangular greater and lesser trochanters are large and wing-shaped and are slightly reflected dorsally. Their broadest part sits just at the base of the head. The comparatively large lesser trochanter has a triangular shape and is situated on the medial side of the shaft. At its distal end, the lesser trochanter is somewhat thickened and bears a rugose tendon insertion mark; a second thickening with tendon insertion mark is present at the proximal end. Both tendon insertion marks are connected by a thin edge. The proximal edge of the lesser trochanter is straight. The greater trochanter is much larger than the lesser and, in contrast to the lesser, has a pointed proximal extension. The proximal and lateral edges of this extension are somewhat broadened and have a rugose surface for tendon insertion.

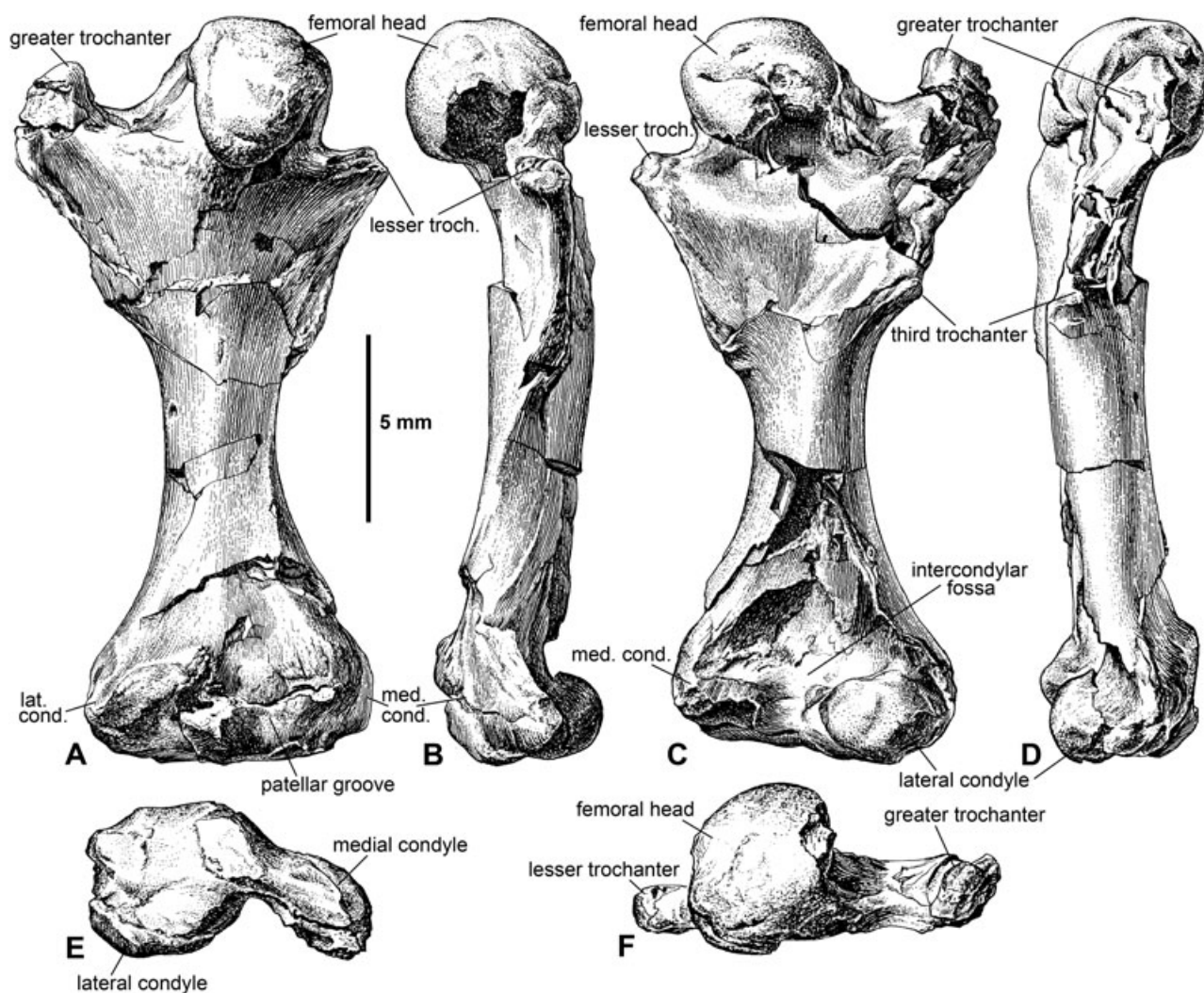


Figure 12. *Haldanodon expectatus*, Gui Mam 47/75. Right femur in: A, anterior (= dorsal); B, medial; C, posterior (= ventral); D, lateral; E, distal and F, proximal view. cond., condyle; lat., lateral; med., medial; troch., trochanter.

At the base of the greater trochanter of Gui Mam 47/75 sits laterally a small third trochanter with a rugose tendon insertion mark. Although almost confluent with the greater trochanter, it is clearly discernible. The connecting edge to the greater trochanter as figured in Figure 12 is now broken.

The distal joint is somewhat narrower than the proximal. It has two well-developed condyles of which the lateral condyle is about twice as large as the medial in both specimens. The lateral condyle is bulbous and the medial condyle is flattened dorsoventrally. On the ventral side, the condyles are well separated by a deep intercondylar fossa. On the dorsal surface, somewhat shifted medially, a shallow depression is detectable in Gui Mam 47/75 (this area is broken in Gui Mam 30/79) which represents the patellar groove. The patellar groove is restricted to the dorsal side and does not wrap around the distal end. A patella has not been found.

Gui Mam 47/75 is about 1.5 times larger than the femur from the skeleton (Gui Mam 30/79) and derives from a much older individual. There are striking age-related differences between both specimens. In Gui Mam 47/75 the greater and lesser trochanter are much stronger and the greater trochanter is more upright whereas it points laterally in Gui Mam 30/79. In the larger femur, both trochanters are separated by deep, saddle-shaped notches from the head that is more rounded than in Gui Mam 30/79. A third trochanter is not detectable in Gui Mam 30/79.

Tibia: The right tibia of Gui Mam 30/79 (Fig. 13) is the only one available of *Haldanodon*; it is preserved on the artificial matrix in a ventral (anterior) aspect. The distal part of the bone is obscured by skull fragments but can be studied from the dorsal side through the transparent plastic. The tibia is rather short, about the same length as the humerus, and is comparatively stout. The shaft has a triangular cross section. The triangular proximal head is widely expanded and appears almost symmetrical; however, the medial facies is partially crushed and collapsed which gives the proximal part of the tibia a broader appearance than it really has. The proximo-lateral tubercle is well developed and prominent but partially damaged. Therefore, it is unclear whether an articulation facet for the proximal end of the fibula was present. The proximal articulation facet is also damaged and does not provide any particular morphological details. On the lateral side of the proximal head a deep triangular sulcus for the attachment of tendons and ligaments is visible. The lateral sulcus extends on the lateral side of the shaft and forms a shallow depression, possibly for extensor muscle insertion. On the medial side of the proximal head a similar sulcus like on the lateral side seems to be present. However, apparently this

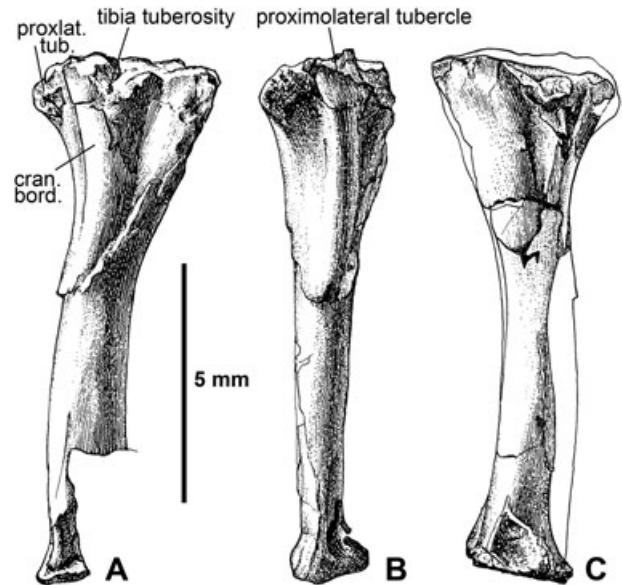


Figure 13. *Haldanodon expectatus*, Gui Mam 30/79. Right tibia in: A, anterior; B, lateral; and C, posterior view. bord., border; cran., cranial; proxlat., proximolateral; tub., tuberosity.

sulcus was at least partially artificially caused by the compression and breakage of the medial flank of the tibia shaft. At the anterior side of the proximal head the tibial tuberosity (insertion place for patellar tendons) is moderately developed; it extends distally as a faint cranial border.

The distal end, which only can be studied through the plastic, is slightly broadened and somewhat damaged. It appears to have an elliptical flat articulation surface. The distal tibial malleolus is not detectable.

Phalanges: Associated with the skeleton several phalanges have been found that cannot be attributed to the hand or foot with certainty. Henkel & Krusat (1980: 215) report three phalanges which were preserved together with the skeleton on the slab of artificial matrix. One of these phalanges (which was embedded between the ulna and femur (Henkel & Krusat, 1980: figs 3 and 4)) in the meantime has been removed from the artificial matrix and is now kept isolated. The phalanx which is still embedded at the distal end of the ulna is exposed in the plantar (ventral) aspect (Fig. 1). The bone is very short and has a semi-circular distal articulation facet with a deep median groove. Almost no shaft is developed, both articulation facets sit very close together. Judging by the shape of the proximal articulation facet, which has a medial ridge, the bone is a second phalanx. In the first phalanx, a median groove (as for example in *Manis javanica*) or a smooth facet for the articulation with the metapodial would be expected. Strongly shortened

second phalanges were observed in the early Miocene pangolin *Necromanis franconica* from the Allier basin in France (Koenigswald & Martin 1990), whereas in extant manids the first phalanges are shorter than the second (Hildebrand, 1995: fig. 21-5). The phalanx which is now kept isolated (Fig. 14A–B) is also very short and is morphologically almost identical to that described above. On the dorsal side of the proximal articulation facet a bony stop is present that prevents the phalanx from hyperextension.

The other phalangeal bone, which is still embedded in the artificial matrix, is located near the distal end of the femur (Fig. 1). It is visible in a ventro-lateral (or ventro-medial) aspect. The bone has a slightly longer shaft than the phalanx embedded at the distal end of the ulna, but the proximal articulation facet clearly

exhibits a median ridge, indicating that it is also a second phalanx. One side of the proximal articulation facet is broken.

In association with a *Haldanodon* maxilla with dentition (Gui Mam 132/74), two terminal phalanges, six phalanges, two metapodials and two small unidentified carpals or tarsals (Figs 14, 15) were found which are attributed to that taxon. The six isolated phalanges are all similar morphologically. They are short and five of them have a semicircular concave proximal articulation facet with a faint median ridge (at least visible on the dorsal part; Fig. 15A–E). Therefore they can be interpreted as second phalanges. One of the phalanges (Fig. 15F) lacks this median ridge and has a smooth proximal articulation facet. It may be interpreted as the first phalanx. The distal articulation fac-

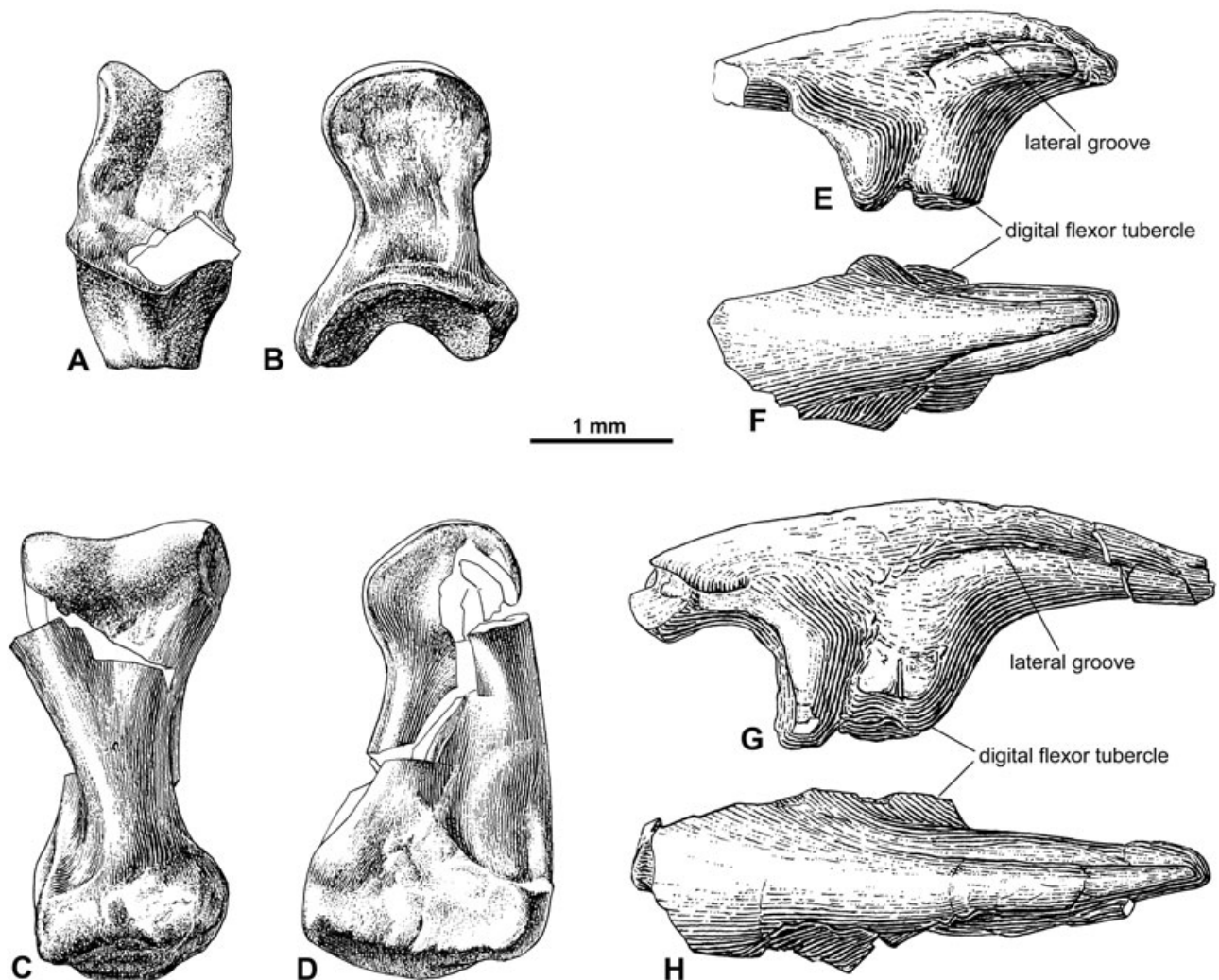


Figure 14. *Haldanodon exspectatus*, phalanges and metapodial in dorsal (A, C, F, H) and side (B, D, E, G) views. A–B, Gui Mam 30/79, phalanx II. C–D, Gui Mam 3012, metapodial probably from central position. Distal articulation facet is facing the top of page in A–D. E–F, Gui Mam 132/74–9, terminal phalanx, probably from medial or lateral position. G–H, Gui Mam 132/74–10, terminal phalanx, probably from central position.

ets of the phalanges are semicircular convex with a deeply cut median groove which corresponds very well with the proximal articulation facet of the terminal phalanges (with median ridge). The notches for the dorsal and ventral tubercles at the proximal articulation facets of the terminal phalanges are well developed.

Both terminal phalanges are only slightly curved. The larger specimen (Fig. 14G–H) is elongate and compressed laterally. On the medial and lateral side two grooves are present for attachment of the horny claw, and on the ventral side the claw has a large

tendon tuberosity. The proximal articulation facet is semicircular with a median ridge; dorsally and ventrally this ridge ends in tuberosities which can be interpreted as blocking mechanisms against overextension when the claw was used for digging.

The smaller terminal phalange (Fig. 14E–F) is considerably shorter, only moderately compressed laterally, and its proximal spur is less elongate (apex is broken off). Morphologically it resembles the larger specimen with lateral and medial groove for horn claw attachment and large tubercles at the ventral side. The semicircular articulation facet is also similar with

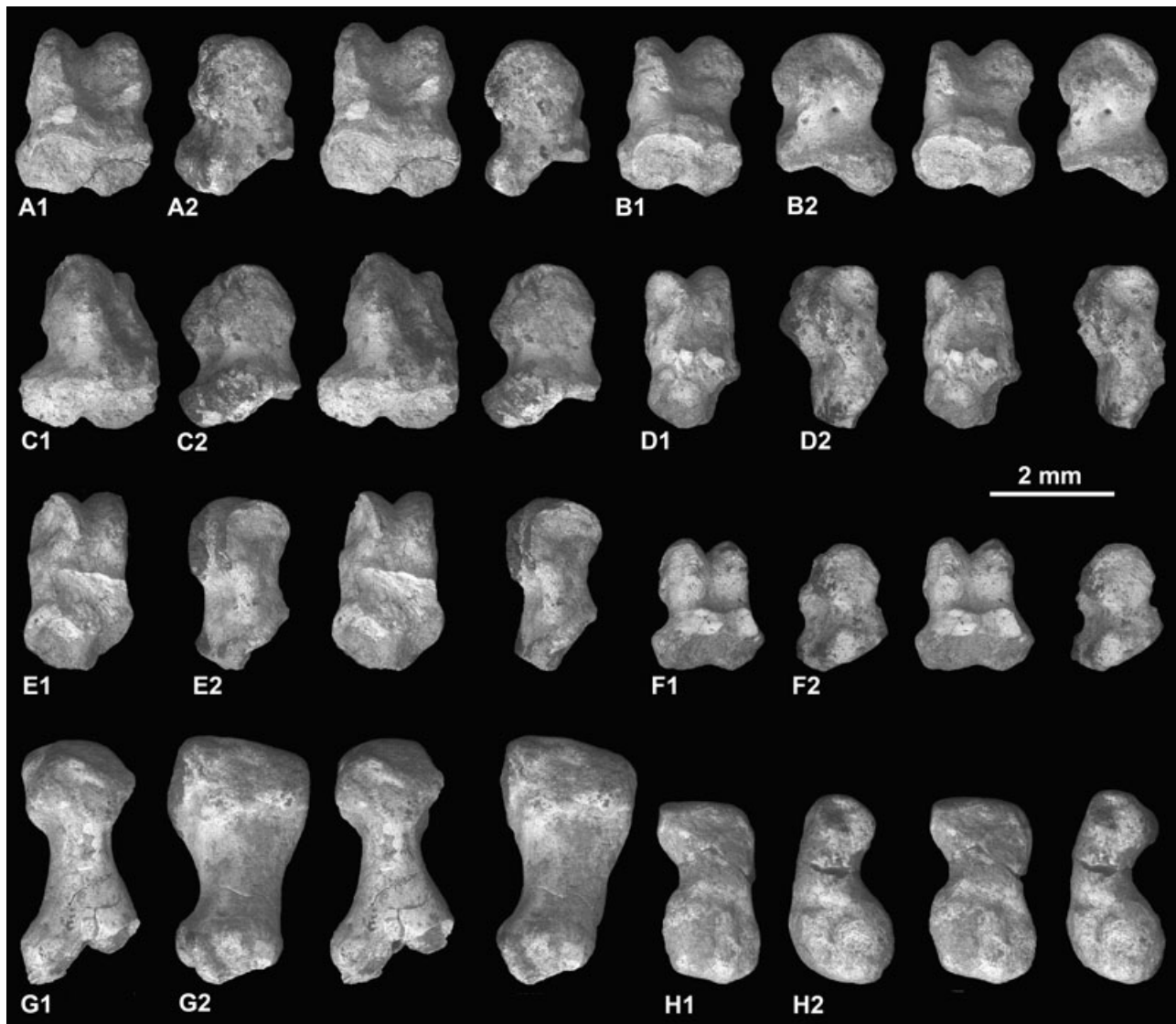


Figure 15. *Haldanodon exspectatus*, Gui Mam 132/74, phalanges. (A–F) and metapodials (G–H) in (1) dorsal and (2) side view (stereo-pairs). Distal articulation facet is facing to the top of page. A, Gui Mam 132/74–1, phalanx II. B, Gui Mam 132/74–2, phalanx II. C, Gui Mam 132/74–3, phalanx II. D, Gui Mam 132/74–4, phalanx II. E, Gui Mam 132/74–5, phalanx II. F, Gui Mam 132/74–6, phalanx I. G, Gui Mam 132/74–7, metapodial, probably from central position. H, Gui Mam 132/74–8, metapodial, from medial or lateral position.

the blocking mechanism at the dorsal and ventral side.

Metapodials: The larger of the two metapodials from Gui Mam 132/74 (Fig. 15G) has a broad proximal and distal articulation facet which are connected by the more slender shaft. The proximal articulation facet is somewhat damaged but it is evident that it originally had a bowl-like shape. On the ventral and lateral/medial sides the broad proximal articulation head bears rugose areas for tendon insertion. The distal head is large and bulbous. It has an asymmetrical oval outline and a slightly convex articulation facet without a median ridge. The lack of a median ridge in the metapodials (which for example is present in *Manis javanica*) is a general feature of *Haldanodon*. On one side the articulation head of the metapodial bears a well-developed tendon tubercle, on the other side a slight depression with rugose surface (also for tendon insertion).

The smaller metapodial bone (Fig. 15H) is more flattened and exhibits less distinct articulation facets; it possibly comes from a more lateral or medial position. The proximal head is broad and bulbous with a flat to slightly convex articulation facet lacking a median ridge. In the distal direction, the bone narrows and broadens again towards the distal head. The distal articulation facet is cylindrical with a slight bowl-like depression on the ventral side. Laterally and medially the distal head bears pits for tendon insertion.

An isolated metapodial (Gui Mam 3012) resembles in shape the larger specimen Gui Mam 132/74–7, but is about 15–20% smaller (Fig. 14C–D); it probably also comes from a central position within the metapodium.

COMPARISON

AXIAL SKELETON

Ribs: In contrast to the monotremes (Starck, 1979: 106), the ribs of *Haldanodon* are double-headed. The putative sternal ribs of *Haldanodon* closely resemble sternal ribs of *Tachyglossus* and *Ornithorhynchus*. Jenkins & Parrington (1976: 393) mention only isolated questionable cervical rib fragments for *Megazostrodon*; therefore a comparison with the ribs of morganucodontids is not possible. Kühne (1956: 112–113) reports proximal ends of double- and single-headed ribs for the tritylodontid *Oligokyphus*, which in a general aspect resemble those of small mammals. Sues & Jenkins (in press) describe for the large tritylodontid cynodont *Kayentatherium wellsi* double-headed thoracal ribs in which the capitular and tubercular facets are separated by a simple constriction, resembling the situation observed in *Haldanodon*. The enigmatic Late Jurassic basal mammal *Fruitafossor windscheffeli* apparently has double headed thoracal

and single headed, mobile lumbar ribs (Luo & Wible, 2005: figs 2a, 3p). Multituberculates (e.g. *Ptilodus kummae*, *Nemegtbaatar gobiensis*) (Krause & Jenkins, 1983; Kielan-Jaworowska & Gambaryan, 1994) and gobiconodontids (e.g. *Gobiconodon ostromi* (Jenkins & Schaff, 1988) have double-headed thoracal ribs which are also present in the eutriconodont *Jeholodens jenkinsi* (Ji, Luo & Ji, 1999) and the holotherians *Zhangheotherium quinquecuspidens* and *Henkelotherium guimarotae* (Krebs, 1991).

PECTORAL GIRDLE

Scapulocoracoid: In the scapula of advanced tritylodontid cynodonts such as *Kayentatherium wellsi* and *Bienotheroides wanhsienensis* an incipient biplanar 'supraspinous fossa' is present (Sues, 1984: fig. 29; Sues & Jenkins, in press: fig. 6C; Sun & Li, 1985) that is missing in *Haldanodon*. As in *Haldanodon*, a well-developed trough-like 'infraspinous fossa' is present that is bordered by the laterally inflected anterior and posterior margins of the scapula. In *Haldanodon*, the postscapular fossa is restricted to the caudo-dorsal extension of the scapula blade, whereas in *Kayentatherium* it extends over the entire caudal border.

As in *Haldanodon*, at the scapula of the Lower Jurassic tritylodontid *Oligokyphus* no prespinal part (= 'supraspinous fossa') is developed. Similarly to the situation in *Haldanodon*, the acromion of *Oligokyphus* is short and does not extend below the glenoid facet. As in *Haldanodon*, the latero-distally orientated glenoid facet of *Oligokyphus* has an oval shape and is formed by the scapula and, at a larger part, by the coracoid. A small triangular procoracoid is present in *Oligokyphus* (Kühne, 1956: 115–116) which is missing in *Haldanodon*.

In the scapulacoracoid of the Early Jurassic stem mammal *Morganucodon* the trough-like 'infraspinous fossa' is also very deep and a 'supraspinous fossa' is absent (Jenkins & Parrington, 1976: 397). Differences to *Haldanodon* are found in the acromion, which represents in *Morganucodon* only a slight thickening along the ventral margin of the scapular flange and which is more prominent in *Haldanodon*. The suture between scapula and coracoid divides the glenoid fossa of *Morganucodon* into two nearly equal parts, whereas the coracoidal part is much smaller in *Haldanodon*. In *Morganucodon* a small procoracoid is present whereas in *Haldanodon* it is completely reduced. The procoracoid has a procoracoid foramen in *Morganucodon* and *Megazostrodon*, but this foramen is absent in *Haldanodon*. The coracoid of *Haldanodon* is rod-like and not a thin and plate-like, posteriorly tapering structure as in *Morganucodon*.

The scapula of the Late Jurassic enigmatic basal mammal *Fruitafossor windscheffeli* resembles that of

Haldanodon with a large 'infraspinous fossa', a well-developed 'subscapular spine' (= posterior margin), and incipient 'scapular spine' (= anterior margin). Similarly to *Haldanodon*, the saddle-shaped glenoid is formed by both the scapula and a separate coracoid (Luo & Wible, 2005).

The monotremes *Tachyglossus* and *Ornithorhynchus* possess a weak 'secondary' scapular spine (Serenó & McKenna, 1995: fig. 4) that here is considered to be homologous to the posterior scapular margin of *Haldanodon*. Caudally of that 'secondary' spine lies a large postscapular fossa that extends over the entire height of the scapula and is widest in its dorsal part. The scapula of *Tachyglossus* is not triangular in shape, but almost rectangular because the acromion is incorporated in the scapula blade. In *Ornithorhynchus* the situation is similar, but the scapula is narrower antero-posteriorly, with a huge hook-like extension (Processus dorsocaudalis; Klima, 1973) at the dorsal side which is pointing distally. In *Ornithorhynchus* the coracoid is comparatively longer than in *Haldanodon*, and in *Tachyglossus* it is more robust.

In Late Cretaceous and Early Cenozoic multituberculates such as *Ptilodus kummae* and cf. *Bulganbaatar* the scapulocoracoid has a reduced coracoid but lacks a 'supraspinous fossa' (Krause & Jenkins, 1983; Sereno & McKenna, 1995). For the scapulae of cf. *Bulganbaatar*, ?*Mesodma*, and two unidentified Late Cretaceous multituberculates from North America a trough-like 'infraspinous fossa' that is bordered by the laterally inflected anterior and posterior scapular margins has been described (Krause & Jenkins, 1983: figs 9, 10; Sereno & McKenna, 1995: figs 3, 4). For the Late Cretaceous multituberculate *Nemegtbaatar gobiensis* from Mongolia a more derived scapulocoracoid with an incipient 'supraspinous fossa' has been described (Kielan-Jaworowska & Gambaryan, 1994).

The Early Cretaceous eutriconodont *Jeholodens jenkinsi* has a much more derived scapula than *Haldanodon* with a scapular spine ending in a robust, peg-like acromion and a fully developed supraspinous fossa (Ji *et al.*, 1999). A large supraspinous fossa is also present in a scapula that is attributed to the Early Cretaceous triconodont *Gobiconodon ostromi* (Jenkins & Schaff, 1988). In *Jeholodens* and *Gobiconodon*, the infraspinous fossa is flat and resembles the therian condition without a laterally reflected posterior scapula margin. The glenoid facets in both taxa are facing ventrally, like in extant therians.

The Early Cretaceous symmetrodont *Zhangheotherium* has a therian-like triangular scapular blade with a well-developed scapular notch that separates it from the ventrally facing glenoid. The scapular spine is very high and, as in other holotherians, ends in a prominent acromion. The supraspinous fossa extends along the entire length of the blade, but is much nar-

rower than the flat infraspinous fossa. In contrast to *Haldanodon* with a peg-like coracoid, *Zhangheotherium* has a hook-like coracoid process (Hu *et al.*, 1997).

The Late Jurassic paurodontid *Henkelotherium guimarotae* has an essentially 'modern' scapula with a high spine and a well-developed supraspinous fossa. The infraspinous fossa is flat and the posterior margin of the scapula is not laterally reflected. The coracoid is greatly reduced and does not participate in the formation of the glenoid facet (Krebs, 1991).

FORELIMB

Humerus: The humerus of the Early Jurassic tritylodontid *Oligokyphus* differs considerably from that of *Haldanodon*. In *Oligokyphus* the humerus is much more slender and the deltopectoral crest is thin and high but not wing-like and does not extend medially. At the proximal head, neither the lesser nor the greater tubercle are separate structures but are confluent with the humeral head (Kühne, 1956: 117–120). As in *Haldanodon*, the lesser tubercle is larger than the greater tubercle, but is not wing-shaped. The humeral shaft is not as strongly twisted in *Oligokyphus* (40°) as in *Haldanodon* (60°). The distal humeral head of *Oligokyphus* is not as broad as that of *Haldanodon* because both epicondyles are less strongly expanded laterally and medially. These differences to *Haldanodon* apply also to the humeri of the trithelodontid *Pachygenelus* sp. indet. (Gow, 2001) and the large tritylodontid *Kayentatherium wellsi* (Sues & Jenkins, in press: fig. 11). Compared to *Oligokyphus* and *Kayentatherium*, the humeral head of *Haldanodon* is more rounded and has a much stronger dorsoventral curvature.

The humerus of *Morganucodon* is much more slender than that of *Haldanodon*. The proximal and distal ends of the *Morganucodon* humerus are twisted about 50° (Jenkins & Parrington, 1976: 400). Besides the slenderness, the most striking differences refer to the development of the deltopectoral crest and other muscle insertion areas which are much stronger and more pronounced in *Haldanodon*. In this regard, *Haldanodon* closely resembles small digging eutherians, such as *Talpa*, *Amblysomus* and *Desmana*, which exhibit a strong development of the deltopectoral crest and other muscle insertions.

The humerus of *Fruitafossor windscheffeli* is very similar to that of *Haldanodon* with its hourglass shape, large deltopectoral crest, and very wide distal portion with well-developed epicondyles. *Fruitafossor* exhibits even stronger adaptations towards a fossorial lifestyle than *Haldanodon*, as are the hypertrophied teres tuberosity and very large supinator crest at the ectepicondyle (Luo & Wible, 2005: fig. 2). The ratio of

epicondylar width to humeral length is slightly larger in *Fruitafossor* (about 65) than in *Haldanodon* (61.4), and *Fruitafossor* has a less pronounced humeral head and more spherical radial and ulnar condyles.

There are striking overall similarities with the humerus of the echidna (*Tachyglossus aculeatus*), particularly the hourglass-like shape, the broad proximal head, and the strongly developed deltopectoral crest. Differences in the distal head between *Haldanodon* and the monotremes *Tachyglossus* and *Ornithorhynchus* concern the more spherical radial condyle that is not synovial with the ulnar condyle in the docodont and its larger entepicondylar foramen. The entepicondyle is considerably broader in both monotremes than in *Haldanodon*. In *Tachyglossus*, proximal and distal ends of the humerus are twisted about 45° to each other. *Ornithorhynchus* differs from *Tachyglossus* and *Haldanodon* by humeral heads that are twisted by 90°.

The multituberculate humerus is characterized by a spherical head, a lesser tubercle that is only slightly smaller than the greater tubercle, and a wide intertubercular groove. In comparison to *Haldanodon*, the multituberculate humeri are more slender and have a narrower distal end. As in *Haldanodon*, ulnar and radial condyle are well separated and no incipient ulnar trochlea is developed (Krause & Jenkins, 1983; Kielan-Jaworowska & Gambaryan, 1994). Kielan-Jaworowska & Gambaryan (1994) estimate the humeral torsion for the genus *Lambdopsalis* as about 35°, and Sereno & McKenna (1995) for *Bulganbaatar* as 15°, which is considerably lower than in *Haldanodon* (60°).

Although the humerus of *Gobiconodon* has a robust deltopectoral crest extending distally beyond the shaft's midpoint and despite its strongly broadened distal end, it appears much more slender than that of *Haldanodon*. A second crest is present on the medial side of the shaft, probably representing the teres tuberosity (attachment of teres major and/or latissimus dorsi muscles). The humeral torsion in *Gobiconodon* is much lower (33°) than in *Haldanodon* (60°). Two isolated trochleae attributed to the humeri of *Gobiconodon* are grooved as in therians (Jenkins & Schaff, 1988) and not bulbous as in *Haldanodon*.

The humerus of *Zhangheotherium* is slender and the torsion of the proximal end relative to the distal end is only about 30°. In contrast to *Haldanodon*, *Zhangheotherium* and *Jeholodens* have more derived humeri with an incipient trochlea for the ulna which represents a therian apomorphy. However, the humeri of both have also prominent spherical radial condyles and weakly-developed ulnar condyles, plesiomorphic characters characteristic for *Haldanodon* and other nonholotherian mammals (Hu *et al.*, 1997, 1998; Ji *et al.*, 1999; Luo & Ji, 2005).

The humerus of *Henkelotherium* is much more slender and has much narrower proximal and distal ends than that of *Haldanodon*. Although the radial and ulnar condyle are clearly separated in an anterior (= ventral) aspect, an incipient ulnar trochlea is present on the posterior (dorsal) side, representing the derived therian condition (Krebs, 1991).

Radius: In contrast to the radii of the tritylodontids *Oligokyphus* and *Kayentatherium* and the stem mammal *Morganucodon*, the radius of *Haldanodon* is straight and not sigmoidally curved (Kühne, 1956: 122; Jenkins & Parrington, 1976: 401; Sues & Jenkins, in press: fig. 13). The *Haldanodon* radius is stouter and does not exhibit the slight groove at the anterior side of the lower third of the shaft which was described for *Morganucodon* by Jenkins & Parrington (1976). In *Oligokyphus* (Kühne, 1956: 122 and text-fig. 56), *Kayentatherium* (Sues & Jenkins, in press: fig. 13a) and *Morganucodon* (Jenkins & Parrington, 1976: 401, figs 8f, 10a–d) the proximal articulation facet is inclined antero-laterally while it is orientated almost perpendicularly to the long axis of the shaft in *Haldanodon*.

In *Tachyglossus* and *Ornithorhynchus*, at the distal end of the radius two articulation facets for the scapholunatum are present, while in *Haldanodon* only one shallow facet is developed. The radius of *Tachyglossus* and *Ornithorhynchus* is more slender than that of *Haldanodon*. In *Haldanodon*, it is shorter than the humerus, whereas in *Tachyglossus* it is longer and in *Ornithorhynchus* it is of the same length. As in *Haldanodon*, the oval proximal articulation facet is orientated perpendicularly to the radius shaft in *Ornithorhynchus* and *Tachyglossus*.

The radius of the multituberculate *Nemegtbaatar gobiensis* widens strongly distally and bears a prominent, triangular styloid process (Kielan-Jaworowska & Gambaryan, 1994). The proximal articulation facet for the radial condyle of the humerus is orientated obliquely (facing antero-dorsally) to the long axis of the shaft, which is also the case in *Ptilodus kummae* (Krause & Jenkins, 1983).

The radius of *Gobiconodon* is more slender than that of *Haldanodon* and its distal end is only slightly wider than the proximal. The outline of the proximal end is elliptical and the articulation facet shallowly concave (Jenkins & Schaff, 1988).

The radius of *Zhangheotherium* is straight and has a distally expanding shaft; its distal end is twice as wide as that of the ulna. The proximal end bears a slightly oblique, oval articulation facet for the radial condyle of the humerus. There is no evidence for a styloid process at the distal end (Hu *et al.*, 1998).

The radius of *Henkelotherium* is slender and almost straight. The shaft is only slightly thickened

distally and in the medio-dorsal corner of the distal joint a small styloid process is developed (Krebs, 1991).

Ulna: In the ulna of *Oligokyphus* and *Morganucodon*, the articulation facet for the ulnar condyle of the humerus is much more semicircular than in *Haldanodon*. In *Haldanodon* both proximal articulation facets of the ulna are very shallow and elongate (proximo-distally). Another difference is evident from the olecranon itself, which is more strongly bent anteriorly in *Oligokyphus* and *Morganucodon* than in *Haldanodon* (Kühne, 1956: 121–123; Jenkins & Parrington, 1976: 402, figs 8e, 10e–h).

The ulna of the basal mammal *Fruitafossor windscheffeli* has a longer olecranon process than that of *Haldanodon* (66% of the ulna portion distal to the pivot of the semilunar notch (Luo & Wible, 2005) vs. 47% in *Haldanodon*) which underlines its extreme adaptation towards a fossorial lifestyle (Hildebrand, 1995).

The ulna of *Tachyglossus* also clearly differs from that of *Haldanodon*. In *Tachyglossus* only one spoon-shaped articulation facet for the ulnar condyle of the humerus is developed. Because the radial condyle of the humerus does not articulate with the ulna, a corresponding articulation facet is absent. The small radial notch is sitting disto-laterally of the facet for the ulnar condyle and has an oval shape in contrast to the elongate (mesio-distally) shape in *Haldanodon*. The spoon-shaped articulation facet for the ulnar condyle of monotremes closely resembles the pattern of early Mesozoic (Triassic) mammals rather than Jurassic holotherians (Jenkins, 1973: 288, fig. 17C). The olecranon of *Tachyglossus* is longer than that of *Haldanodon*, less bulbous and strongly bent anteriorly. Like in *Tachyglossus*, the ulna of *Ornithorhynchus* has only one bowl-like articulation facet for the humerus. The olecranon of *Ornithorhynchus* greatly differs from that of *Haldanodon* by its large wing-shaped lateral and medial extensions.

In the multituberculates *Catopsalis joineri* and *Nemegtbaatar gobiensis* the articular surface for the ulnar condyle is nearly semicircular (Krause & Jenkins, 1983; Kielan-Jaworowska & Gambaryan, 1994) and clearly differs from the shallow facet in the ulna of *Haldanodon*.

Like the ulna of *Haldanodon*, the ulna of *Gobiconodon* has a proximally widely expanded olecranon. The shaft of the ulna is anteroposteriorly broad and the articular surface for the ulnar condyle is comparatively shallow (Jenkins & Schaff, 1988).

In *Zhangheotherium* (Hu *et al.*, 1998) and *Jeholodens* (Z.-X. Luo, pers. comm., 2004) the articular surface for the ulnar condyle is also almost semicircular. A very similar, therian-like shape of the articular

surface is present in *Henkelotherium* (Krebs, 1991), reflecting a more parasagittal posture of the limb.

PELVIC GIRDLE

Ilium: *Haldanodon* has a typical blade-like mammalian ilium, whereas it is shovel-like in cynodonts. Another mammalian feature present in the *Haldanodon* ilium and lacking in that of cynodonts is the gluteal line that separates the dorsal gluteal from the ventral iliacus origin areas (Sues, 1984; Sues & Jenkins, in press). In *Oligokyphus* and *morganucodontids* these mammalian features are present (Kühne, 1956; Jenkins & Parrington, 1976), although their ilia are much more slender than that of *Haldanodon*.

The ilium of *Tachyglossus* is quite similar to that of *Haldanodon* in shape and robustness. The gluteal line is more prominent in *Tachyglossus* and the psoas tubercle and iliopectic eminence are much stronger, whereas the sacral tuber is considerably smaller.

The multituberculate ilium exhibits the typical mammalian features as elongated, rod-like shape and a lateral gluteal line (Krause & Jenkins, 1983; Kielan-Jaworowska & Gambaryan, 1994). However, the proportions of the very gracile multituberculate ilium are so different from Gui Mam 3011 that an attribution to the multituberculates can be ruled out with certainty.

Gobiconodon, *Jeholodens* and *Zhangheotherium* all exhibit the typical mammalian configuration of a rod-like, elongate ilium with gluteal line but their ilia are much more slender and gracile than that of *Haldanodon* (Jenkins & Schaff, 1988; Hu *et al.*, 1997; Ji *et al.*, 1999; Luo & Ji, 2005). The same applies to the ilium of *Henkelotherium* (Krebs, 1991), therefore a dryolestoid origin of Gui Mam 3011 can be ruled out.

HINDLIMB

Femur: The femur of *Oligokyphus* (Kühne, 1956: 125–127, text-fig. 58) and *Morganucodon* (Jenkins & Parrington, 1976: 407f, figs 12, 13b, c, e) is much more slender than that of *Haldanodon*. Like in *Haldanodon*, the greater and lesser trochanters are wing-shaped but not as strongly enlarged, so that the proximal head of the femur is less expanded. The distal end is much narrower and less bulbous than in *Haldanodon*, giving the humerus a more gracile appearance. Like in *Haldanodon*, the femoral heads of *Oligokyphus* and *Morganucodon* are somewhat reflected dorsally and medially. In both, *Oligokyphus* and *Morganucodon*, the distal condyles are more flattened than in *Haldanodon* and therefore are more similar to the situation observed in monotremes (e.g. *Tachyglossus*). In *Haldanodon*, the patellar facies is shifted medially, while it sits more laterally of the shaft-midline in *Morganucodon* in a dorsal aspect.

The femur of *Haldanodon* differs significantly from that of *Tachyglossus*. In *Haldanodon*, the greater and lesser trochanters are much more pronounced and are extending more strongly laterally and medially. In *Tachyglossus*, the humerus shaft is compressed ventro-dorsally and has almost the same width in its entire length. Distal and proximal ends are hardly broader than the shaft, and at the proximal head the trochanters form only moderate lateral and medial extensions. In *Haldanodon*, the shaft has an oval cross section and proximal and distal heads are much broader, giving the femur a more hourglass appearance. In *Haldanodon*, only a small and not very distinct patellar facies is developed which is shifted medially; in *Tachyglossus*, the patellar facies is much larger and sits in the middle of the distal head.

The multituberculate femur is characterized by a spherical head with an extensive articular surface and a long femoral neck that forms an angle of 50–60° to the shaft as well as by a subtrochanteric 'lesser' tubercle (Kielan-Jaworowska & Gambaryan, 1994). In *Haldanodon* the femoral neck is very short. The multituberculate femur has a prominent greater trochanter that extends beyond the head and a prominent, plate-like lesser trochanter that strongly protrudes ventrally. In *Haldanodon*, the greater trochanter does not extend beyond the head; the trochanters are triangular and emerge symmetrically on both sides of the head. The cross section of the femoral shaft of *Ptilodus kummae* is not oval as in *Haldanodon*, but circular at midlength and more elliptical proximally (Krause & Jenkins, 1983).

The femur of *Zhangheotherium* is much more slender than that of *Haldanodon* and its spherical head is set off from the shaft by a well-defined neck (Hu *et al.*, 1997; Luo & Ji, 2005). The femur of *Jeholodens* lacks such a neck and has a very weakly developed patellar groove at the distal end (Ji *et al.*, 1999). In this regard it more closely resembles the femur of *Haldanodon*. Lesser and greater trochanters are considerably smaller than in *Haldanodon*, and also the distal end is much narrower. The femur of *Gobiconodon* has a bulbous head that is set off from the shaft by a flat broad neck. The lesser trochanter forms a broad flange that bears a deep fossa on its dorsal side adjacent to the shaft, a unique structure that has not been observed in other mammals. The (broken) greater trochanter probably was large and a third trochanter is present on the lateral side of the shaft (Jenkins & Schaff, 1988).

The femur of *Henkelotherium* is much more slender than that of *Haldanodon* and has a straight shaft with a round cross section. The hemispherical femoral head is set off the shaft by a well-defined neck (angle about 30°) and has a fovea for a femoral head ligament. The larger trochanter is strong and equals the femoral

head in height from which it is separated by a notch. The lesser trochanter that protrudes medially is also strong and originates at the base of the neck (Krebs, 1991).

Tibia: The tibia of *Oligokyphus* is more slender than that of *Haldanodon*. Compared to the slender shaft, it has a broad proximal head which widens abruptly (particularly on the lateral side; Kühne, 1956: text-fig. 59). The tibia of *Morganucodon* is also more gracile than that of *Haldanodon* and has a more asymmetrical proximal head due to the large, laterally projecting process for the fibula. In an anterior aspect, the proximal part of the tibia of *Haldanodon* is less bowed laterally than that of *Morganucodon*. The depression on the lateral side [possibly for extensor muscle origin (Jenkins & Parrington, 1976)] is shallower in *Haldanodon* than in *Morganucodon*.

The tibia of *Tachyglossus* differs considerably from that of *Haldanodon*. Its proximal head is much broader and less clearly triangular in shape (cross section) because the cranial border is weakly developed at the best. There are no lateral and medial sulci at the proximal head in *Tachyglossus*. The caudal aspect is not flat as in *Haldanodon* but somewhat rounded. At the distal head, the broadest part is not situated in the distal end because it tapers slightly distally. As a general impression, the outlines and morphological features of the monotreme tibia appear less distinctive than in the *Haldanodon* tibia.

The multituberculate tibia is characterized by a strongly asymmetrical proximal end, with a small medial and a large lateral facet. A large, hook-like process extends from the proximal end laterally and bears a facet for the fibula. The tibiae of *Chulsanbaatar vulgaris* and *Ptilodus kummae* are much more slender than that of *Haldanodon* and are bent laterally (*Chulsanbaatar*) or are sigmoidally curved (*Ptilodus*) (Krause & Jenkins, 1983; Kielan-Jaworowska & Gambaryan, 1994).

The tibiae of *Gobiconodon* and *Zhangheotherium* are more slender than that of *Haldanodon* and lack a distinct cranial border and anterior tibial tuberosity (*Zhangheotherium*) (Jenkins & Schaff, 1988; Luo & Ji, 2005). The tibia of *Henkelotherium* is also much more slender than that of *Haldanodon* and has a narrower proximal end. The tibial tuberosity is more prominent than in *Zhangheotherium*, but weaker than in *Haldanodon*. In contrast to *Haldanodon*, at the distal end a comparatively large medial malleolus is present.

Metapodials and phalanges: The terminal phalanges of *Oligokyphus* described by Kühne (1956: 135, text-fig. 65) resemble those of *Haldanodon*: they are moderately compressed laterally, are not split and possess a groove on the lateral and medial side for horn claw attachment.

The metacarpals and proximal phalanges of digits 2–4 of *Fruitafossor windscheffeli* are proximo-distally shortened like in *Haldanodon*. Differing from *Haldanodon*, the terminal phalanges of *Fruitafossor* are dorso-ventrally flattened, broad, and nearly spatulate. Their apex is not bifid, and they possess large flexor tubercles (Luo & Wible, 2005: fig. 2I).

The claws of semifossorial *Ornithorhynchus* are dorsoventrally flattened and straight (with lateral and medial groove) in the hand and moderately laterally compressed and slightly curved in the foot. In fossorial *Tachyglossus* the claws are flattened and are only very slightly curved in hand and foot and have no median slit. Both monotremes have proximo-distally shortened metapodials and first and second phalanges.

The fossorial mole *Talpa europaea* and the golden moles *Chrysochloris capensis* and *Calcochloris obtusirostris* have strongly dorso-ventrally flattened claws at the hands which have a median groove (*Talpa*) or slit. The claws of the feet are not flattened but a median groove or slit is always present. The claws of the semiaquatic and semifossorial talpids *Galemys pyrenaicus* and *Desmana moschata* are laterally compressed and slender. They have a median groove and are only slightly curved; lateral and medial grooves are not developed. The claws of the foot are considerably longer than those of the hand. The claws of the scratch-digging manids (e.g. *Manis javanica*) and dasypodids (e.g. *Tatusia novemcincta*) are moderately curved and laterally compressed and are very similar to that of *Haldanodon*. The manid claws have a deep median slit while *Tatusia novemcincta* has lateral grooves in its terminal phalanges. Manids and dasypodids have proximo-distally shortened metapodials and first and second phalanges.

DISCUSSION

PHYLOGENETIC POSITION OF *HALDANODON* *EXSPECTATUS*

The coracoid part of the scapulocoracoid of *Haldanodon* is more derived than that of advanced cynodonts (*Oligokyphus*, *Kayentatherium*; Kühne, 1956; Sues, 1984; Sues & Jenkins, in press) and the stem mammals *Morganucodon* and *Megazostrodon* (Jenkins & Parrington, 1976) by complete reduction of the procoracoid and the absence of the procoracoid foramen. In monotremes, a procoracoid is present, but it lacks the procoracoid foramen (Klima, 1973). The scapular part is essentially at the same evolutionary level as in advanced cynodonts and morganucodontids by retention of a trough-like 'infraspinous fossa' that is bordered by the laterally deflected anterior and posterior scapular margins. Similarly to *Haldanodon*, a supraspinous fossa is lacking in morganucodontids (Jenkins

& Parrington, 1976). In contrast to these basal mammals, an incipient 'supraspinous fossa' is present in some eucynodonts (Jenkins, 1971; Kemp, 1980; Sues, 1984; Sun & Li, 1985) which caused problems in its interpretation as a mammalian synapomorphic character (Sues & Jenkins, in press). A biplanar supraspinous fossa is also absent in multituberculates (Krause & Jenkins, 1983; Sereno & McKenna, 1995) and monotremes, whereas it is present in eutriconodonts and trechnotherians.

Traditionally, the cranial border of the scapula of nontherian mammals is considered homologous to the scapular spine of therians (Romer, 1922; Jenkins & Weijs, 1979). This view has recently been contested by Sánchez-Villagra & Maier (2002, 2003) on the basis of embryological studies on marsupials. The part of the therian scapular spine that is located dorsally of the acromion is now considered a neomorphic structure that is not homologous to the cranial border of the scapula of nontherians. According to this reinterpretation of the therian scapular spine, it has become questionable whether the incipient fossa on the cranial side of the eucynodont scapula can be homologized with the therian supraspinous fossa. The scapular spine and supraspinous fossa of the holotherians *Zhangheotherium* (Hu *et al.*, 1997, 1998) and *Henkelotherium* (Krebs, 1991), and of Early Cretaceous eutriconodonts (Jenkins & Crompton, 1979; Ji *et al.*, 1999) are here regarded as homologous with the corresponding structures of therians. The trough-like 'infraspinous fossa' of *Haldanodon*, eucynodonts (Sues, 1984; Sues & Jenkins in press), tritylodontids (Kühne, 1956), morganucodontids (Jenkins & Parrington, 1976), *Fruitafossor* (Luo & Wible, 2005), and multituberculates (Krause & Jenkins, 1983; Sereno & McKenna, 1995) differs from the flat infraspinous fossa of holotherians and only its ventral portion is here considered to be homologous to the latter.

According to Sues & Jenkins (in press), a postscapular fossa is not a general mammalian character, but occurs in fossorial taxa such as some edentates and forms with a powerful forelimb stroke. It is present in *Kayentatherium* and incipiently developed in basal eucynodonts (Jenkins, 1971). In *Haldanodon* the postscapular fossa is restricted to the dorsal portion of the scapula with a wing-like extension in a posterior direction.

The postero-lateral orientation of the scapular glenoid in *Haldanodon* closely resembles the situation observed in monotremes. This is most likely correlated to the fossorial adaptation (see below), because in advanced eucynodonts such as *Kayentatherium*, this facet is already mainly ventrally orientated as in more derived mammals (Sues & Jenkins, in press).

The humerus of *Haldanodon* is more derived than that of advanced eucynodonts such as *Kayentatherium*

(Sues, 1984; Sues & Jenkins, in press), *Oligokyphus* (Kühne, 1956) and *Pachygenelus* (Gow, 2001) as well as of morganucodontids (Jenkins & Parrington, 1976) in that the greater and lesser tubercle are not confluent with the humeral head but represent distinct features. Further derived characters of *Haldanodon* are a more rounded humeral head and a clear set off of the head from the shaft. At its distal joint, the *Haldanodon* humerus represents the stage of advanced cynodonts and of the stem mammal *Morganucodon* with well-separated and individual radial and ulnar condyles and the lack of an olecranon fossa on the dorsal (= posterior) side. A similar condition with well-separated condyles is also characteristic for multituberculates (Kielan-Jaworowska & Gambaryan, 1994; Gambaryan & Kielan-Jaworowska, 1997, *contra* Sereno & McKenna, 1995).

The basic features of the ulna of *Haldanodon* and other early mammals such as sigmoidal curvature, antero-posteriorly narrow shaft, and longitudinal grooves, are already present in basal eucynodonts (Jenkins, 1971: figs 31, 32; Sues & Jenkins, in press). An ossified olecranon process occurs in tritylodontids and basal mammals, whereas more basal eucynodonts probably had cartilaginous processes. As discussed below, the large olecranon process of *Haldanodon* most likely is related to its fossorial behaviour.

As in *Morganucodon*, the distal end of the ulna for radial contact is rounded in *Haldanodon*, and the contact facet on the radius is flat. This implies that translation at the distal radioulnar joint was possible, in contrast to tritylodontids with a flat contact surface at the distal end of the ulna (Sues & Jenkins, in press).

The shape of the ilium of *Haldanodon* represents the basic mammalian condition that is already established in tritylodontids (*Oligokyphus*) and morganucodontids (Kühne, 1956; Jenkins & Parrington, 1976). The robustness of the *Haldanodon* ilium and its very strong sacral articulation are related to the fossorial adaptation.

The configuration of the *Haldanodon* femur corresponds widely to that of *Morganucodon* and other nontherian mammals except multituberculates. The proximal head of the femur of *Haldanodon* is more rounded than in eucynodonts with an ovoid caput (Sues & Jenkins, in press), but less hemispheroidal than in *Morganucodon*. The shape of the femoral head most probably is related to its fossorial adaptation (Reed, 1951). The femoral neck of *Haldanodon* is less developed than that of *Gobiconodon*, multituberculates and trechnotherians. The extent of the intertrochanteric fossa is difficult to estimate in *Haldanodon* because this area is collapsed in both specimens that were available for study. The configuration of the femoral trochanters in *Haldanodon* corresponds to that observed in *Morganucodon* where both trochant-

ers are situated almost at the same height at the femoral shaft. In basal eucynodonts, the lesser trochanter sits ventral and distal to the greater trochanter, and in the tritylodontid *Kayentatherium* it is shifted medially but is still distal of the greater trochanter (Sues & Jenkins, in press). In *Haldanodon*, a well-developed notch separates the greater trochanter from the femoral head, which has been cited as an apomorphic character by Kühne (1956: 126) and Hopson & Kitching (2001: 31). Sues & Jenkins (in press) note that a slight indentation is present in basal eucynodonts (Jenkins, 1971: fig. 48A–B), and that the degree of separation is rather an effect of ossification of the proximal end of the trochanter. As in morganucodontids and early nontherian mammals, the greater trochanter of *Haldanodon* is proximally directed and possesses a pronounced apex, and thus the notch between trochanter and femoral head is accentuated.

The addition of three new characters and previously unknown scores for *Haldanodon* to the matrix of Luo, Kielan-Jaworowska & Cifelli (2002) and partial re-scoring (see Appendix) of postcranial character states corroborated the position of *Haldanodon* above the node of morganucodontids as sister-taxon of *Hadrocodium* plus *Kuehneotherium* and crown group Mammalia (*sensu* Luo *et al.*, 2002) (Fig. 16).

LIMB POSTURE OF *HALDANODON EXSPECTATUS*

On the humerus of *Haldanodon*, the lesser tubercle is much larger, wider and protrudes more strongly medially over the shaft of the humerus than the greater tubercle. This is typical for animals with primary abducted forelimbs, such as lacertilians, cynodonts, morganucodontids, and monotremes, whereas in mammals with parasagittal limbs the lesser tubercle is smaller (and narrower) than the greater tubercle (Gambaryan & Kielan-Jaworowska, 1997). In terrestrial tetrapods with a primary sprawling posture the humerus shows a relatively high torsion (up to 60°), a wide intertubercular groove, a lesser tubercle that is wider than the greater one, and the condylar type of the elbow joint, with spherical radial condyle and oval, convex ulnar condyle (Gambaryan & Kielan-Jaworowska, 1997: 39). Among fossorial eutherians humeral torsion occurs only in Chrysochloridae. Because in *Haldanodon* the lesser tubercle is much larger than the greater tubercle and the humerus is strongly twisted, a sprawling gait can be certainly postulated for the docodont. Despite the very lateral orientation of their humeri, the limb movements of extant monotremes are more similar to that of therians than that of lepidosaurs (Jenkins, 1970; Pridmore, 1985: 64). According to Pridmore (1985: 70f), the locomotion of modern monotremes indicates that ancestral mammals were substantially 'therian' in

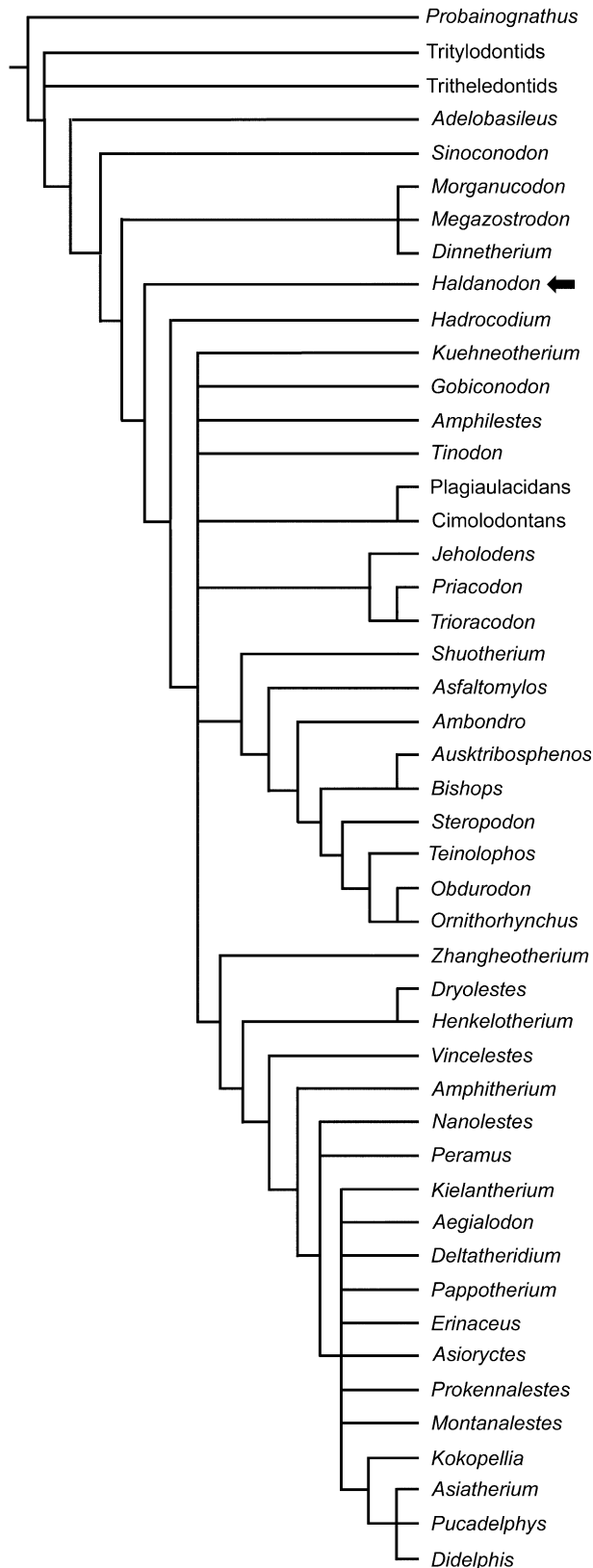


Figure 16. Strict consensus tree of 27 equally parsimonious trees for early mammals based on 280 cranio-mandibular and postcranial characters using PAUP 4.0b10 with heuristic branch-and bound search, set at random with 1000 replicates; starting seed = 1794832392. All characters unordered and with equal weight. Each of the 27 equally parsimonious trees has: Treelength = 956, CI = 0.500, RI = 0.763. *Haldanodon* (arrow) appears above the node of morganucodontids as sister taxon of the common ancestor of *Hadrocodium* and living mammals plus all of its descendants (node 2 in Luo *et al.*, 2002: figs 1, 2). For character states and score for *Haldanodon* see the Appendix.

their locomotory mode. However, this does not mean that these forms possessed an erect locomotor posture.

A fossorial adaptation has considerable influence on the limb orientation as for example in *Talpa* with a secondary sprawling stance of the forelimbs (Gambaryan & Kielan-Jaworowska, 1997). This is the most probable reason for the modifications in limb bone morphology and limb orientation of monotremes in comparison to *Morganucodon* and other early mammals, of which Pridmore (1985: 72) stated that they '... possessed limb orientations essentially similar to those observed in locomotively generalized extant therian mammals.' Depending on the position of *Haldanodon* on the cladogram, its limb bone features do not necessarily represent a plesiomorphic 'reptilian' heritage, but may well be correlated with the fossorial adaptation of the docodont.

LIFESTYLE OF *HALDANODON EXSPECTATUS*

Fossorial adaptations are rare among Mesozoic mammals, and they generally have rather unspecialized postcranial skeletons. Therefore for most taxa with known postcranium either a more scansorial [e.g. *Henkelotherium*, *Eomaia* and *Sinodelphis* (Krebs, 1991; Vázquez-Molinero *et al.*, 2001; Ji *et al.*, 2002; Luo *et al.*, 2003)] or more terrestrial [e.g. *Repenomamus*, *Sinobaatar* and *Zhangheotherium* (Hu *et al.* 1997, 1998, 2005; Hu & Wang, 2002)] lifestyle is assumed. A stout humerus with prominent deltopectoral crest and comparatively wide distal end has been interpreted as fossorial adaptation in a Cretaceous and two early Palaeogene taeniolabidoid multituberculates (Miao, 1988; Kielan-Jaworowska, 1989; Kielan-Jaworowska & Qi, 1990). A remarkable exception is the recently described Late Jurassic basal mammal *Fruitafossor windscheffeli* with strong fossorial adaptations in forelimb and manus (Luo & Wible, 2005) that are strikingly similar to those of modern scratch diggers and *Haldanodon*. Due to the incomplete fossil record of early stem-mammals, particularly from the Middle Jurassic, it is difficult to say if these fossorial adapta-

tions at least partially represent a retention of the plesiomorphic condition observed in many eucynodonts or a secondary specialization.

The humerus of *Haldanodon*, with its very broad proximal and distal heads and the enlarged trochanters, immediately evokes comparison with talpids (e.g. *Talpa* and *Scapanus*) or monotremes (*Tachyglossus*, *Ornithorhynchus*). Based on these similarities, Krusat (1991) postulated a fossorial lifestyle for *Haldanodon*, and also referred to the wedge-like shape of the skull of *Haldanodon* which probably was used like a shovel lifting loose soil away over its back.

In talpids (e.g. *Talpa*, *Scapanus*, *Galemys*, *Desmana*) and the chrysochlorid *Amblysomus hottentotus* the scapula is strongly elongated and narrow which is interpreted as an adaptation to their fossorial lifestyle (Reed, 1951: 539). The scapulocoracoid of *Haldanodon* only with limitations can be compared to the scapula of therian mammals. However, it exhibits a striking similarity to the scapula of the Oligocene palaeonodont *Xenocranium* (Rose & Emry, 1983), even if the relevant structures may not be homologous. In the *Xenocranium* scapula, apart from the scapular spine, a 'secondary spine' at the posterior margin of the scapular blade is developed, that functionally corresponds to the laterally bent posterior margin of the *Haldanodon* scapula. A 'secondary spine' characterizes also the scapula of digging xenarthrans and some fossorial rodents such as the Spalacidae (Gambaryan, 1960; Lehmann, 1963). Compared to the fossorial monotreme *Tachyglossus*, the scapulocoracoid of *Haldanodon* appears rather long and narrow; it more closely resembles in shape the scapulocoracoid of the semiaquatic and semifossorial *Ornithorhynchus*, but has a shorter wing-like posterior extension at the dorsal side. Fossorial talpids and *Tachyglossus* and *Ornithorhynchus* have an oval glenoid facet limiting the movements of the humerus. In the semicursorial *Sorex* the glenoid fossa is a segment of a spherical surface and allows movements of the spherical head of the humerus in all directions (Reed, 1951: 536). The oval shape of the glenoid fossa of *Haldanodon* points to a fossorial adaptation.

The humerus of *Haldanodon* is very similar in shape and proportions to that of *Tachyglossus* and *Ornithorhynchus*. In *Ornithorhynchus*, the twist of the proximal and distal head is 90°, which is much greater than in *Haldanodon* and *Tachyglossus*. The humerus of *Talpa*, which is almost as broad as long with its greatly enlarged deltopectoral crest, represents an extreme fossorial adaptation, while *Desmana* and *Galemys* exhibit only moderate expansion of the deltopectoral crest and other muscle insertion planes.

The proximal humeral head of fossorial talpids, chrysochlorids (e.g. *Amblysomus*), and palaeonodonts

(*Epoicotherium*, *Xenocranium*; Rose & Emry, 1983) is elliptical while it is spherical in semicursorial soricids (Reed, 1951). *Haldanodon* has an elliptical humeral head. This shape represents the plesiomorphic mammalian condition but also can be interpreted as an adaptation towards a fossorial lifestyle. Together with the oval glenoid facet a hinge-like shoulder joint is formed that limits the range of movement of the humerus to a mainly antero-posterior direction. This is typical for fossorial taxa. In specialized fossorial mammals such as monotremes and various fossil and extant therians that abduct their forelimbs during digging, the distal end of the humerus, and especially the entepicondyle, is strongly expanded (Gambaryan & Kielan-Jaworowska, 1997: 33). *Haldanodon* also possesses an enlarged entepicondyle.

Like in talpids and chrysochlorids, which mainly use their front limbs for digging, in *Haldanodon* the humerus is considerably stronger than the femur. Therefore it can be postulated that *Haldanodon* mainly used its front limbs for digging and that the hind limbs fixed the body while burrowing (see below).

A large olecranon as present in the ulna of *Haldanodon* is another indicator for a fossorial lifestyle because it acts as in-lever of the triceps muscle. Hildebrand (1995) determined a range of relative length of the olecranon compared to the entire ulna length between 20 and 75% for fossorial taxa; the olecranon (with semilunar notch) of *Haldanodon* is 47% of the ulnar length and falls well within this range.

The very short first and second phalanges of *Haldanodon* are typical for scratch-digging mammals such as armadillos, fossil and extant pangolins (e.g. *Manis javanica*, *Necromanis franconica*; Koenigswald & Martin, 1990), and palaeonodonts (*Epoicotherium*, *Xenocranium*; Rose & Emry, 1983). The two terminal phalanges which were found in association with other footbones and a maxilla of *Haldanodon* are pointed, only slightly curved and moderately laterally compressed. Morphologically, they resemble the claws of pangolins (*Manis*) except for the median slit that is not present in *Haldanodon*; instead of the median slit, *Haldanodon* has a groove on each side of the claw for attachment of the horn claw. *Manis* is a typical scratch-digger (Hildebrand, 1995), in contrast to *Talpa* which digs in soft soil and has broad and flattened terminal phalanges. All strongly fossorial talpids have bifid terminal phalanges, and 'the grooved and bifid phalanx is an obvious adaptation for strengthening the union of phalanx and claw, and the distribution of this modification within the Talpidae is in correlation with the fossorial activities of the genera' (Reed, 1951: 556). Furthermore, in all fossorial talpids (except *Uropsilus*; Reed, 1951: 555; further references therein) the claws of the hand are spatulate,

which is a very characteristic feature and easy to recognize. The two claws of Gui Mam 132/74 are not spatulate (however, it is not possible to attribute them to a pes or manus), and among several hundred isolated probable mammalian phalanges from the Guimarota coal, which were recovered by screen-washing, no spatulate phalanges were been detected. This makes it very probable that the hand of *Haldanodon* was adapted to scratch digging rather than to the shovel digging style of *Talpa* and other fossorial talpids. The lateral and dorsal shapes of the terminal phalanges of *Haldanodon* correspond closely to those that are typical for fossorial small mammals as demonstrated by McLeod & Rose (1993) by eigenshape analysis. After McLeod & Rose (1993), fossorial taxa are distinguished by shallower (= dorso-ventrally compressed) ungual phalanges with a distinctive broadly curving dorsal margin and a relatively undifferentiated extensor tubercle.

The claws of the hands of *Ornithorhynchus* are moderately flattened (claws of feet are not flattened) and, like *Haldanodon*, have a groove on each side for attachment of the horn claw. In *Tachyglossus* the claws of hands and feet are flattened but have no median slit or lateral grooves.

Stout and comparatively short ilia that are strongly fused to a high number of sacral vertebrae are typical for fossorial mammals such as *Manis* and *Tachyglossus*. (Hildebrand, 1995).

In talpids the hind legs are not used for digging, but for fixing the body when the soil is scratched loose with the hand. Nevertheless, digging adaptations are also evident in the shape of the femur, as the proximal end of the femur is wider and the three trochanters are more strongly developed in the talpids *Scapanus* and *Neurotrichus* than in the soricid *Sorex* (Reed, 1951: 573). The femur of *Ornithorhynchus* like that of *Haldanodon* has enlarged wing-shaped trochanters at the proximal head and a broad distal head. This is also in accordance with a fossorial and possibly semiaquatic lifestyle of *Haldanodon*.

Another adaptation for a fossorial lifestyle of *Haldanodon* is the short and comparatively stout tibia. A short tibia (and resulting short hind leg) is an adaptation towards powerful locomotion with a corresponding loss of speed, and the shorter hind leg can be manipulated more easily during burrowing (Reed, 1951: 575). Therefore it can be concluded that *Haldanodon* most probably was a fossorial and possibly semiaquatic animal, comparable to the habits of *Ornithorhynchus* and desmans. This kind of lifestyle appears more suitable for the swampy environment of the Guimarota ecosystem (Martin & Krebs, 2000; Kielan-Jaworowska, Cifelli & Luo, 2004) than that of a talpid with a permanent life in subterranean burrows as postulated by Krusat (1991).

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APPENDIX

Scores for postcranial characters 128–169 from the matrix presented by Luo *et al.* (2002) for *Haldanodon exspectatus*. Characters with asterisk * have been rescored and new characters added to the matrix are marked by X in order to keep the original numbering.

128. Interclavicle in adults: (0) present (not preserved, but its presence can be inferred after insertion pit on coracoid): *Haldanodon*; (1) absent.
129. Contact relationships in adults between the interclavicle and the sternal manubrium: (0) two elements distinct from each other, posterior end of interclavicle abuts anterior border of manubrium; (1) two elements distinct from each other, the interclavicle broadly overlaps the ventral side of the manubrium; (2) complete fusion of the embryonic membraneous and endochondral elements; (?) not preserved: *Haldanodon*.
130. Cranial margin of the interclavicle: (0) anterior border is emarginated or flat; (1) with a median process; (?) not preserved: *Haldanodon*.
131. Claviculo-sternal apparatus joint: (0) immobile; (1) mobile; (?) not preserved: *Haldanodon*.
132. Acromio-clavicular joint (as inferred from the articulation facet on the acromion): (0) extensive and rigid articulation: *Haldanodon*; (1) limited articulation.
133. Curvature of the clavicle: (0) boomerang-shaped; (1) slightly curved; (?) not preserved: *Haldanodon*.
134. Scapula – supraspinous fossa: (0) absent (acromion extending from the dorsal border of scapula, and is positioned anterior to glenoid):

- Haldanodon*; (1) weakly developed (present only along a part of the scapula, and acromion positioned lateral to the glenoid); (2) fully developed and present along the entire dorsal border of the scapula.
- 134X. Scapula – infraspinous fossa. New character with the following states: (0) trough-like and bordered by laterally reflected anterior and posterior scapula margins: *Haldanodon*, *Probainognathus* (Romer & Lewis, 1973) tritylodontids, trithelodontids (Sereno & McKenna, 1995, 1996), *Sinoconodon*, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus* [not very deep but bordered by laterally reflected anterior and posterior scapula margins], cimolodontans; (1) flat, scapular margins not laterally reflected: *Gobiconodon*, *Jeholodens*, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Pucadelphys*, *Didelphis*, *Erinaceus*; (?) unknown: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Asfaltomylos*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *plagiaulacidans*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Nanolestes*, *Peramus*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.
135. Scapula – acromion process: (0) short stump (level with the glenoid or behind the glenoid): *Haldanodon*; (1) hook-like and extending below the glenoid.
136. Scapula – a distinctive fossa for the teres major muscle on the lateral aspect of the scapular plate: (0) absent: *Haldanodon*, *Ornithorhynchus**; (1) present.
- 136X. Scapula – postscapular fossa. New character with the following states: (0) present: *Haldanodon*, *Ornithorhynchus*; (1) absent: *Probainognathus* (Romer & Lewis, 1973), trithelodontids (Sereno & McKenna, 1995, 1996), *Morganucodon*, *Megazostrodon*, *Jeholodens*, cimolodontans, *Zhangheotherium*, *Henkelotherium*, *Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*. (0/1 polymorphic): tritylodontids [(0) *Kayentatherium* (1) *Bienotheroides*]; (?) unknown: *Adelobasileus*, *Morganucodon*, *Dinnetherium*, *Sinoconodon*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Asfaltomylos*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Gobiconodon*, *Amphilestes*, *Priacodon*, *Trioracodon*, *Haramiyavia*, *plagiaulacidans*, *Tinodon*, *Dryolestes*, *Amphitherium*, *Nanolestes*, *Peramus*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.
137. Procoracoid (as a separate element in adults): (0) present; (1) fused to the sternal apparatus (Klima, 1973) and absent in adult: *Haldanodon*.
138. Procoracoid foramen: (0) present; (1) absent [assuming the procoracoid is fused to the sternal apparatus in living therians (Klima, 1973)]: *Haldanodon*.
139. Coracoid: (0) large, with posterior process: *Haldanodon*; (1) small, without posterior process.
140. Size of the anteriormost sternal element ('manubrium') relative to the succeeding sternbrae in the sternal apparatus in adults: (0) large; (1) small; (?) unknown: *Haldanodon*.
141. Orientation ('facing' of the articular surface) of the glenoid (relative to the plane of the axis of the scapula): (0) nearly parallel to the long axis of the scapula and facing posterolaterally: *Haldanodon*; (1) oblique to the long axis of the scapula and facing more posteriorly; (2) articular surface of glenoid is perpendicular to the main axis of scapula and facing posterolaterally.
142. Shape and curvature of the glenoid: (0) saddle-shaped, oval and elongate: *Haldanodon*; (1) uniformly concave and more rounded in outline.
143. Medial surface (transverse profile) of the scapula: (0) convex: *Haldanodon*; (1) flat (planar).
- Forelimb*
144. Humeral head: (0) subspherical, weakly inflected: *Haldanodon*; (1) spherical and strongly inflected.
145. Intertubercular groove that separates deltopectoral crest from lesser tubercle: (0) shallow and broad intertubercular groove: *Haldanodon*; (1) narrow and deep intertubercular groove.
146. Size of the lesser tubercle of humerus (relative to the greater tubercle): (0) wider than the greater tubercle: *Haldanodon*; (1) narrower than the greater tubercle.
147. Torsion between the proximal and distal ends of the humerus: (0) strong (more than 30°): *Haldanodon*; (1) moderate (30–15°); (2) weak (less than 15°).
148. Ventral extension of the deltopectoral crest or position of deltoid tuberosity: (0) not extending below the midpoint of the humeral shaft: *Haldanodon**, *Probainognathus*, trithelodontids, *Sinoconodon*, *Morganucodon*, *Megazostrodon*, cimolodontans, *Dryolestes**, *Henkelotherium*,

- Vincelestes*, *Asiatherium*, *Didelphis*, *Pucadelphys*, *Erinaceus*; (1) Extending ventrally (distally) past the midpoint of the humeral shaft: *Ornithorhynchus*, *Gobiconodon*, *Jeholodens*, *Priacodon*, *Zhangheotherium*; (0/1 polymorphic) tritylodontids [*Kayentatherium** (0); *Oligokyphus** (1)]; (?) unknown: *Adelobasileus*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Asfaltomylos*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, *Haramiyavia*, plagiaulacidans, *Tinodon*, *Amphitherium*, *Nanolestes*, *Peramus*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.
- 148X. Development of the teres tuberosity. New character with the following character states: (0) indistinct or absent: *Probainognathus* (Romer & Lewis, 1973: fig. 15), trithelodontids, *Jeholodens*, *Zhangheotherium*, *Dryolestes*, *Asiatherium* (Szalay & Trofimov, 1996: figs 14, 15), *Didelphis*, *Erinaceus*; (1) above midpoint of shaft: tritylodontids, *Morganucodon*, *Megazostrodon*, *Ornithorhynchus*, *Gobiconodon*, *Priacodon*, cimolodontans, *Henkelotherium*, *Vincelestes*; (2): extending ventrally (distally) beyond the midpoint of shaft: *Haldanodon*; (?) unknown: *Adelobasileus*, *Sinoconodon*, *Dinnetherium*, *Hadrocodium*, *Kuehneotherium*, *Shuotherium*, *Asfaltomylos*, *Ambondro*, *Ausktribosphenos*, *Bishops*, *Steropodon*, *Teinolophos*, *Obdurodon*, *Amphilestes*, *Trioracodon*, *Haramiyavia*, plagiaulacidans, *Tinodon*, *Amphitherium*, *Nanolestes*, *Peramus*, *Kielantherium*, *Aegialodon*, *Deltatheridium*, *Kokopellia*, *Pucadelphys*, *Pappotherium*, *Asioryctes*, *Prokennalestes*, *Montanalestes*.
149. Ulnar articulation of the distal humerus: (0) bulbous ulnar condyle: *Haldanodon*; (1) cylindrical trochlea (in posterior view) with vestigial ulnar condyle (in anterior view); (2) cylindrical trochlea without ulnar condyle (cylindrical trochlea has extended to the antero-ventral side).
150. Radial articulation of the distal humerus: (0) distinct and rounded condyle in both anterior (ventral) and posterior (dorsal) aspects of the structure that does not form a continuous synovial surface with the ulnar articulation in the antero-ventral view of the humerus: *Haldanodon*; (1) radial articulation forms a rounded condyle anteriorly but its posterior surface is nearly cylindrical; (2) capitulum (radial articulating structure that forms continuous synovial surface with ulnar trochlea; the surface is cylindrical in both anterior and posterior aspects).
151. Entepicondyle and ectepicondyle of the humerus: (0) robust: *Haldanodon*; (1) weak; (0/1) polymorphic.
152. Rectangular shelf for the supinator ridge extended from the ectepicondyle: (0) absent: *Haldanodon*; (1) present.
153. Styloid process of the radius: (0) weak: *Haldanodon*; (1) strong.
154. Enlargement of the scaphoid with a distomedial projection: (0) absent; (1) present; (?) not preserved: *Haldanodon*.
155. Size and shape of the hamate (unciform) in the wrist: (0) anteroposteriorly compressed (wider than long in dorsal view); (1) mediolaterally compressed (wider than long in dorsal view); (?) not preserved: *Haldanodon*.
- Pelvic girdle*
156. Acetabular dorsal emargination: (0) open (emarginated); (1) closed (with a complete rim); (?) not preserved: *Haldanodon*.
157. Sutures of the ilium, ischium, and pubis within the acetabulum in adults: (0) unfused: *Haldanodon* (judged after the suture at ilium); (1) fused.
158. Ischiatic dorsal margin and tuberosity: (0) dorsal margin concave (emarginated) and ischiatic tuberosity present; (1) dorsal margin concave and ischiatic tubercle hypertrophied; (2) dorsal margin straight and ischiatic tubercle small; (?) not preserved: *Haldanodon*.
- Hind limb*
159. Head of the femur is inflected and set off from the shaft by a neck: (0) neck absent (and head orientated dorsally): *Haldanodon*; (1) neck present and head inflected medially; (2) head spherical and inflected.
160. Fovea for the acetabular ligament on femoral head: (0) absent: *Haldanodon*; (1) present.
161. Greater trochanter: (0) directed dorsolaterally: *Haldanodon*; (1) directed dorsally.
162. Orientation of the lesser trochanter: (0) on medial side of shaft: *Haldanodon*; (1) on the ventromedial or ventral side of the shaft.
163. Size of the lesser trochanter: (0) large: *Haldanodon*; (1) small.
164. Patellar facet ('groove') of the femur: (0) absent; (1) shallow and slightly developed: *Haldanodon*; (2) well developed.
165. Proximolateral tubercle or tuberosity of the tibia: (0) large and hook-like: *Haldanodon*; (1) indistinct.

166. Distal tibial malleolus: (0) weak: *Haldanodon*; (1) distinct.
167. Fibula contacting distal end of the femur: (0) present; (1) absent; (?) not preserved: *Haldanodon*.
168. Distal fibular styloid process: (0) weak or absent; (1) distinct; (?) not preserved: *Haldanodon*.
169. Fibula contacting the calcaneus: (0) extensive contact; (1) reduced; (2) mortise and tendon contact of fibula to the ankle; (?) not preserved: *Haldanodon*.

Ankle joint characters 170–179 and other postcranial characters 180–181 are not preserved in *Haldanodon*.