scala vestibuli of the cochlea leads skull-conducted vibrations to produce significant fluid displacement within the cochlea, and hence basilar membrane stimulation[25]. Bone-conducted hearing is consistent with the fossorial lifestyle postulated for *Lambdopsalis* on the basis of cranial and postcranial evidence[5,26]. □

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Cretaceous multituberculate skeleton and the early evolution of the mammalian shoulder girdle

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A Cretaceous eucosmodont multituberculate mammal skeleton has been found in Mongolia with all of the bony elements of the shoulder girdle in place. This specimen demonstrates a different forelimb stance from that recently hypothesized for another Cretaceous eucosmodont. Primitively, it retains a separate ossified interclavicle, as in monotremes and non-mammalian cynodonts. In other respects it shares with therians and their extinct allies key features associated with mobility of the pectoral girdle and shoulder joint during locomotion, and a more parasagittal forelimb posture. This locomotor transformation appears to have evolved just once among the common ancestors of multituberculates and therians, some time before the Late Jurassic.
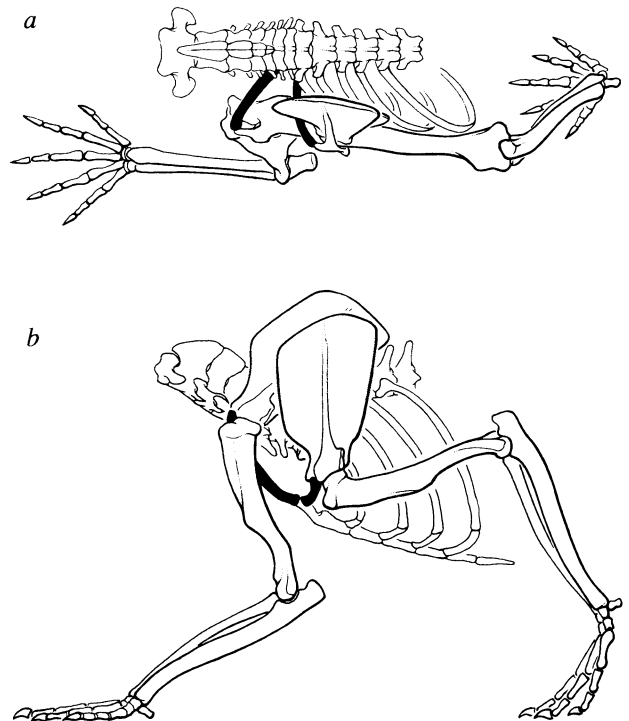
FIG. 1 *a, b,* Excursion of the left pectoral girdle and forelimb relative to the vertebral column and ribcage in a walking opossum (*Didelphis virginiana*) in dorsal (*a*) and lateral (*b*) views[1].

Early in mammalian evolution, locomotor function of the shoulder and forelimb was remodelled[1-3]. The shoulder girdle began to move with the forelimb during the stride, and the forelimb was repositioned under the shoulder girdle so that the forefoot landed closer to the midline (Fig. 1). During the stride's propulsive phase, shoulder girdle and shoulder joint rotate posteroventrally, with only limited motion (flexion) at the shoulder and elbow joints. Because the elbow joint remains closer to the body wall, its hingelike movements are tightly constrained by a trochlear humero-ulnar joint[4]. This locomotor pattern characterizes most living therian mammals and profoundly influences manoeuvrability and gait[5].

A more ancient locomotor pattern is present in non-mammalian cynodonts[6] and primitive Mesozoic mammals[7], retained in modified form in living monotremes[8,9]. In the ancient pattern, the shoulder blade is firmly anchored to a median interclavicle or sternum, the socket of the shoulder girdle is broadly exposed in lateral view, the humerus projects away from the body axis at an angle of at least 45°, and the manus is positioned lateral to the shoulder girdle. The humerus generates much of the propulsive component of the stride by retraction and/or long-axis rotation[8]. The elbow joint is not constrained by a trochlear articulation.

Important clues regarding the architecture of the shoulder girdle and forelimb in many Mesozoic mammals have been discovered over the years[10-16], and the fate of bones that were reduced or eliminated in the course of this functional reorganization has been traced[17,18]. Nonetheless, the stance of anterior limbs has been hypothesized from incomplete specimens to conform with the ancient pattern[16].

A skeleton of a Mongolian Cretaceous multituberculate, PSS-MAE-103 [type Djadokhta Formation (Campanian), from 'ruins locality', Bayn Dzak], preserves the entire pectoral girdle, manubrium sterni and proximal segments of the forelimb (Fig. 2). It clearly pertains to a eucosmodontine taeniolabidoid multituberculate, provisionally referred to *Bulganbaatar nemegtbaataroides*[19] (Fig. 2a). Clavicle and interclavicle (not

FIG. 2 PSS-MAE-103 (Paleontology Section, Mongolian Academy of Sciences), cf. *Bulganbaatar nemegtbaataroides*. *a*. Stereo figure of the articulated skull and anterior part of the skeleton in anterior view; *b–d*, anterior (*b*), dorsal (*c*) and ventral (*d*) views of the anterior part of the skeleton. Identification is based upon proportionately long premaxillary postero-lateral process, nasal–parietal contact, U-shaped frontoparietal suture, anterior orbital shelf, rounded zygomatic arch with lateral crest, single ventrolaterally positioned infraorbital foramen, palatal vacuities, absence of palatal thickenings, deep jugular fossa, and advanced M^1 cusp formula. Abbreviations: ac, acromion; ax, axis; c, clavicle; co, coracoid; dc, deltopectoral crest; dv, dorsal vertebrae; ec, ectepicondyle; en, entepicondyle; enf, entepicondylar foramen; gl, glenoid; gr, coracoid groove; gt, greater tuberosity; h, humerus; hh, humeral head; ic, interclavicle; isf, incipient supraspinous fossa; lt, lesser tuberosity; ms, manubrium sterni; pco, procoracoid; pcof, procoracoid foramen; pp, posterior process of coracoid; r, rib; ra, radius; sc, scapulocoracoid; sf, supraspinous fossa; ss, scapular spine; ssp, secondary scapular spine; uc, ulnar condyle; ul, ulna. Scale bars, 1 cm.
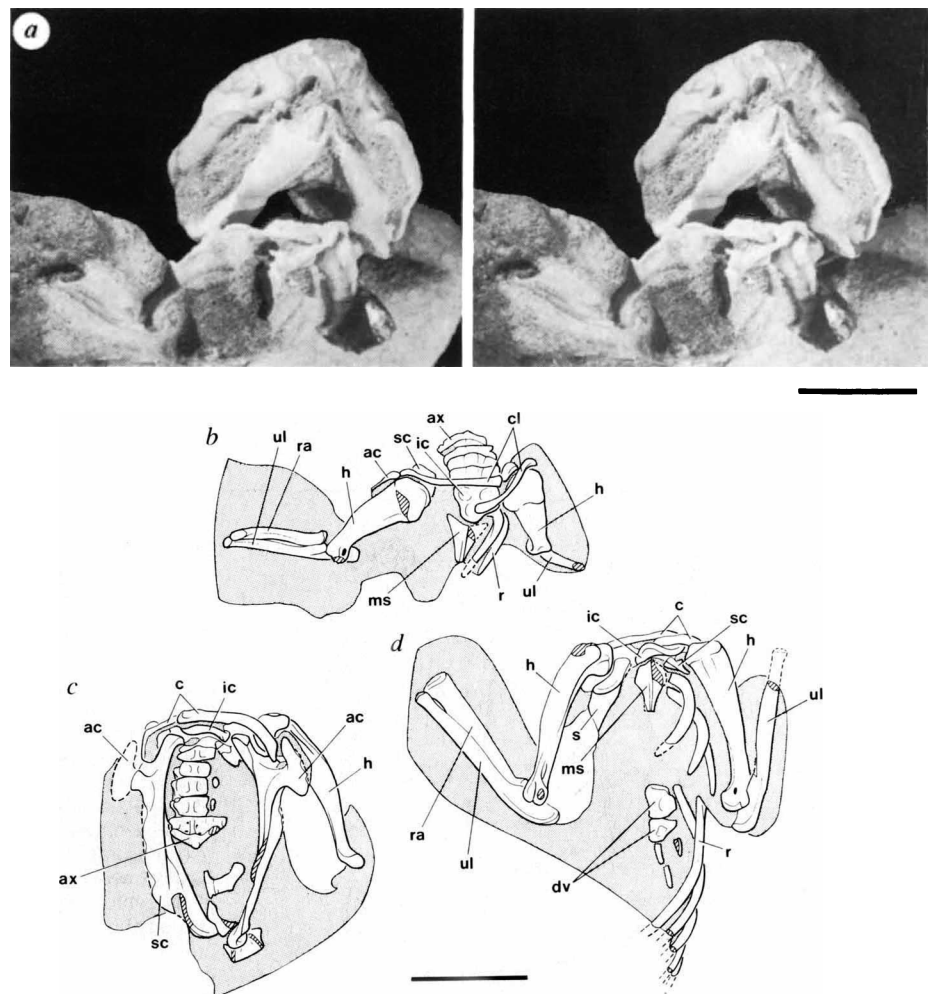
represented in previously described Mongolian Cretaceous multituberculates[16]), and scapulocoracoid are present. The long scapular blade is deeply concave laterally, as in previously reported multituberculate scapulae[14,16], and has an elongate acromial process. Scapula and coracoid fuse relatively early in development in multituberculates. There is no trace of a scapulo-coracoid suture in PSS-MAE-103 or other undamaged specimens[10,16]. The multituberculate coracoid forms only the ventral tip of the glenoid fossa. Unlike other mammals, there is no development of a coracoid posterior process (Fig. 3*a*, *c*). The slender, curved clavicle is strap-shaped throughout most of its length but becomes rod-shaped near its articulation with the cloverleaf-shaped interclavicle, which is arched anteroposteriorly (Fig. 3*a*). The interclavicle has shallow anterior fossae for articulation with the clavicles. It has a short ventral process that rests on a keeled manubrium sterni (Fig. 3*b*). The proximal end of the humerus is dominated by a bulbous head, with rounded tuberosities on its anterior margin (Fig. 3*d*, *e*). As in other multituberculate humeri[12,14,16,20], the distal end has a broad inter-condylar groove, prominent ulnar condyle, and moderate-sized epicondyles. There is less humeral shaft torsion (approximately 15°) (Fig. 3*f*) than in the basal mammals (*Morganucodon*)[7] or monotremes[9]. Forearm bones equal the humerus and scapula in length (Fig. 3; Table 1).

A separate ossified interclavicle in multituberculates is a primitive feature shared with non-mammalian cynodonts and monotremes[6,10,17,21]. In therian mammals, in contrast, the dermal portion of the interclavicle never appears in development, and the endochondral portion fuses with the manubrium sterni[17,18].

In other respects the multituberculate pectoral girdle is structurally advanced[10,20], resembling that in therians (Fig. 4) and not so abducted as hypothesized recently[16].

TABLE 1   Measurements of PSS-MAE-103, cf. *Bulganbaatar nemegtbaataroides*

	Size (mm)
Skull	
Length	26.5
Scapulocoracoid	
Length	17.5
Length of glenoid	4.4
Width of glenoid	1.4
Length of acromion	5.2
Width of blade	(3.0)
Clavicle	
Length	9.0
Mid-shaft, minimum width	0.5
Mid-shaft, width	0.9
Medial end, diameter	1.0
Interclavicle	
Depth	3.3
Width	4.3
Manubrium sterni	
Length	5.4
Width	(5.0)
Humerus	
Length	15.7
Maximum diameter of head	3.0
Width of distal end	3.5
Radius	
Length	12.0
Width of distal end	2.5
Ulna	
Length	16.0
Width of distal end	1.2

Length, width and depth are maximum values unless stated otherwise. Parentheses indicate estimation.
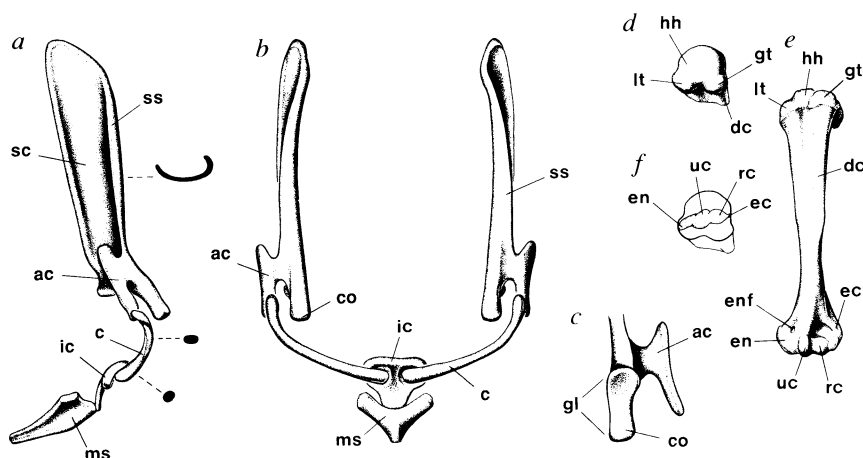
FIG. 3 Scaled reconstruction of the pectoral girdle, manubrium sterni and humerus of PSS-MAE-103, cf. *Bulganbaatar nemegtbaataroides*. a, b, Pectoral girdle and manubrium sterni, in right lateral (a) and anterior (b) views with cross-sections of the scapular blade and clavicle; c, right glenoid and acromion in posteroventral view (enlarged 20% compared with other figures); d, e, left humerus in proximal (d), and anterior (e) views; f, left humerus in proximal view showing orientation of distal end. See Fig. 2 for abbreviations.

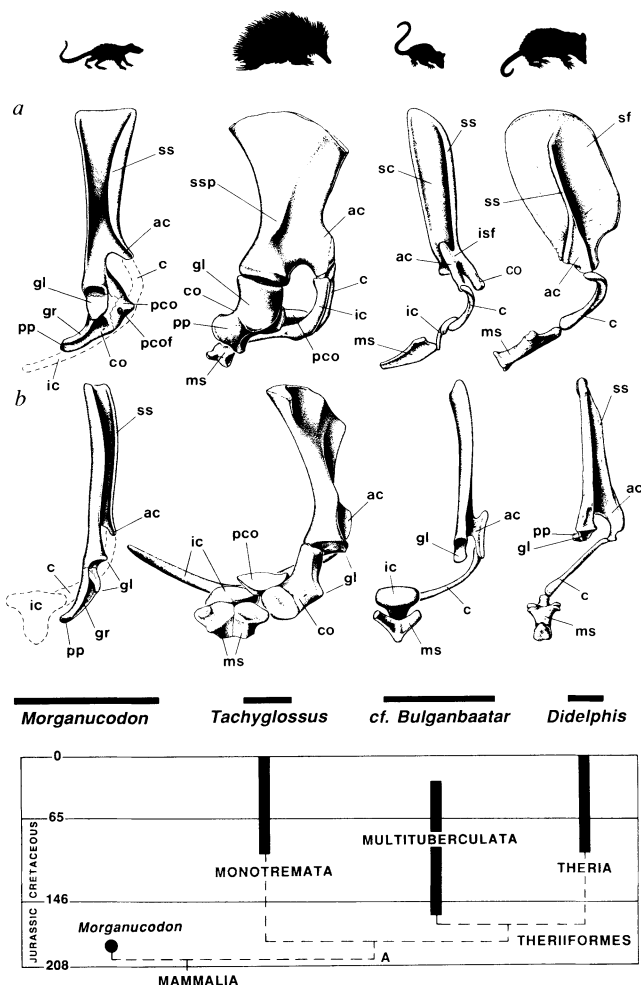Morganucodon   Tachyglossus   cf. Bulganbaatar   Didelphis

FIG. 4 Early evolution of the mammalian pectoral girdle as shown by comparison of an early mammal (*Morganucodon*), monotreme (subadult *Tachyglossus* with open scapulocoracoid and intrasternal sutures), multituberculate (cf. *Bulganbaatar*), and therian (*Didelphis*) in lateral (a) and posterior (b) views. See Fig. 2 for abbreviations. Scale bars, 1 cm. Solid bars show known stratigraphic range. Apomorphies (22) in the pectoral girdle are listed below, using *Morganucodon*[7] and tritylodonts[30] as successive outgroups. Node A: scapulocoracoid suture fused; procoracoid foramen absent; coracoid groove absent. Theriiformes[25]: acromion and scapular spine positioned lateral to the glenoid (=incipient supraspinous fossa)[2]; coracoid posterior process reduced (equal to, or shorter than, length of coracoid glenoid); glenoid width reduced relative to humeral head[2]; coracoid glenoid faces posteroventrally[2,3]; coracoid glenoid concave (rather than concavoconvex); procoracoid very reduced, lost or fused with manubrium sterni[2,25]; clavicle medial end rod-shaped. Theria: crescentic supraspinous fossa along entire length of scapular blade[2,3]; acromion recurved to parallel scapular blade; separate interclavicle absent (=claviculosternal contact present)[2,3]. Monotremata: coracosternal contact; coracoid and procoracoid overlap interclavicle; clavicle and interclavicle fused; interclavicle lateral process long, contacting acromion; interclavicle posterior process fan-shaped. Multituberculata: coracoid glenoid subrectangular (rather than piriform); coracoid posterior process absent; interclavicle cloverleaf-shaped; interclavicle arched anteroposteriorly.

Several features are present in PSS-MAE-103 that in therians increase the mobility of the shoulder girdle[1]. These include reduction of the procoracoid and the posterior process of the coracoid, posteroventral position of the acromion adjacent to the shoulder joint, and mobile clavicle–interclavicle joint. The procoracoid and coracoid, reduced in early development in therians[18,22], are not present as separate ossifications in adult multituberculates. Interpretation of clavicle–interclavicle joint mobility is based on smooth, rod-shaped medial ends of the clavicles (not striated and flattened as they are in non-mammalian cynodonts[6,14]) and open clavicular depression on the interclavicle. Together, these structural features disassociate the

clavicle from the anterior margin of the shoulder blade so it can function as a mobile strut with a pivot at the sternum. In noncursorial therians, the clavicle follows an angular excursion of as much as 40° during a fast walk[1,2] (Fig. 1).

Additional features are present that in therians appear to increase the range of motion at the shoulder joint[1]. These include the concave surface of the coracoid portion of the glenoid (not saddle-shaped as in non-mammalian cynodonts[6], basal mammals[7] and monotremes[3,6]) and the reduction in transverse (or anteroposterior) width of the glenoid socket to about one-half the diameter of the humeral head (Table 1). The shoulder joint's ball-and-socket architecture and narrow glenoid in multituberculates and therians may allow a greater range of humeral movements[12].

The humerus and elbow joint were positioned closer to the body wall than observed in monotremes[8,9] or reconstructed in non-mammalian cynodonts[6] or basal mammals[7]. This is indicated by marked ventral (not lateral) orientation of the glenoid, reduction in size of humeral epicondyles, and hingelike form of the elbow joint (suggested by prominent, narrow ulnar condyle and broad intercondylar groove on the distal end of the humerus, approaching the form of the therian trochlear joint[4]) (Fig. 3e).

Controversy surrounding phylogenetic relationships among multituberculates, monotremes and therians[23–25] is partly due to incomplete fossil remains of Mesozoic multituberculates[26] and monotremes and extreme transformation of skull and dentition in Cenozoic monotremes[27]. Few cranial or dental characters

support alternative resolutions. Traditionally, multituberculates have been grouped with monotremes and various extinct Mesozoic mammals as 'prototherians', based on interpretations of the bony composition of the side wall of the braincase. However, homology of sidewall ossification[28] and its presence in multituberculates[29] have recently been challenged. Here we suggest that persuasive character evidence is provided by the postcranial skeleton[3,25]. Six characters from the pectoral girdle and forelimb support a closer relationship among multituberculates, therians and their allies (*Gobiconodon*[13] and the dryolestid *Henkelotherium*[15]) than between any of these taxa and monotremes (Fig. 4). Parallel evolution of therian-like shoulder girdles of mammals cannot be invoked until one or more of the aforementioned taxa that exhibit an advanced condition are linked cladistically to taxa, such as monotremes, that lack such features. We suggest that a mobile pectoral girdle and shoulder joint and a forelimb posture with the elbow near the body wall arose only once, some time before the Late Jurassic, in a common ancestor of multituberculates, therians and their extinct allies. □

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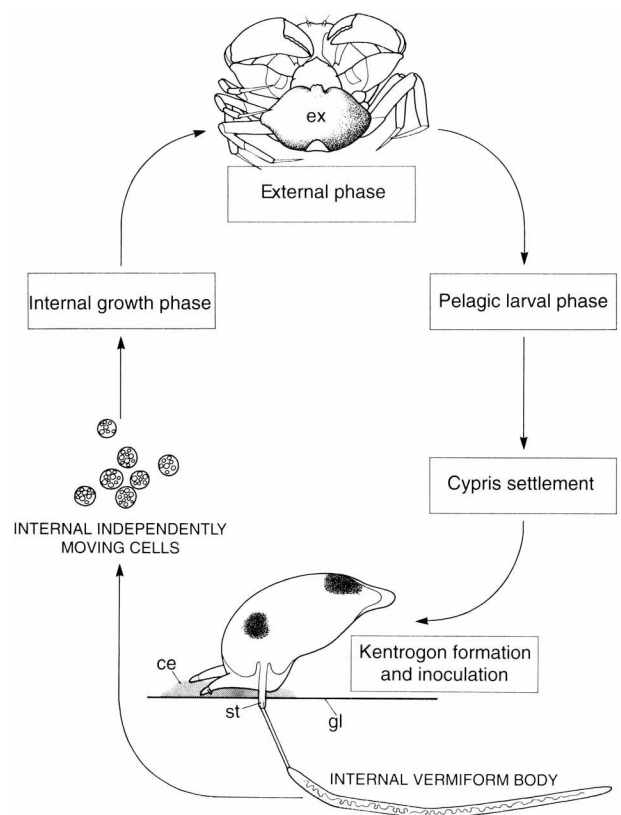30. Sues, H. D. thesis, Harvard Univ. (1983).

A new motile, multicellular stage involved in host invasion by parasitic barnacles (Rhizocephala)

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RHIZOCEPHALANS are barnacles (Cirripedia), but are extremely specialized for parasitic life on decapod crustaceans. A cypris larva settles and develops into a new instar, the kentrogon, which inoculates the host with the parasite. The very early primordial parasite has been argued to consist solely of embryonic stem cells or even eggs[1], but the true nature of this unknown stage has remained a puzzle for more than a century[2]. We present data from *in vitro* experiments on the rhizocephalan *Loxothylacus panopaei* documenting that, unlike previous postulations, the recently injected parasite is not naked embryonic cells, but has the form of a motile, vermiform body, enclosed in an acellular sheath. After a period of maturation the vermiform body splits up into a number of naked and independently moving cells, which in our *in vitro* experiments disperse by amoeboid movements. This suggests that, *in vivo*, the cells disperse in the haemolymph of the host crab, where each has the potential to develop into an adult parasite, although in most cases only one will succeed.

FIG. 1 The generalized life cycle of *Loxothylacus panopaei*. Attached beneath the abdomen of the host crab, the external parasite (externa, ex), up to 1 cm wide, releases broods of nauplius larvae. The lecithotrophic larvae pass through four nauplius stages until they finally reach the cypris stage (200 μm long). The cypris, a larval type unique for cirripedes, terminates the pelagic phase by settling on the gill of a prospective host. A kentrogon (150 μm long) develops underneath the cuticle of the settled cypris. The kentrogon develops a hollow cuticular stylet (st), that penetrates the cuticle of the gill (gl). The stylet then serves as a hypodermic needle to inoculate a motile, vermiform body. A period of vigorous motions results in the detachment of the vermiform body from the stylet. After less than 24 h the motions slow down and the core of the vermiform body begins to split up into independently moving single cells. The sheath of the vermiform body eventually ruptures and the parasite cells escape to the surroundings. The fate of these cells is not known but it seems likely that each has the potential to develop into an adult organism, although only one will normally succeed. ce, Cement. (Drawn by Beth Beyerholm.)