ing to distinctive radiogenic isotope ratios after sufficient time); such a process would have minimal effects on oxygen isotope ratios. □

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Monotreme affinities and low-frequency hearing suggested by multituberculate ear

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MULTITUBERCULATES are an extinct, dentally distinctive group of Mesozoic/early Cenozoic mammals of uncertain affinities[1]. We report here the discovery of a multituberculate ectotympanic bone, associated with the malleus in original life position, from two exquisitely preserved auditory regions. This documents, to our knowledge for the first time, incorporation of the angular and prearticular bones (jaw components in non-mammalian tetrapods) into the middle ear of multituberculates, favouring the hypothesized single origin of the ossicular chain in mammals[2,3]. Morphology and orientation of these elements are strikingly similar to those of the extant egg-laying platypus and echidnas, suggesting a unique common ancestry of these forms[4], an affiliation once generally discredited[5–8] but regaining some recent support[9,10]. The structure of these new multituberculate auditory ossicles, in conjuction with a greatly inflated vestibule and an uncoiled cochlea, implies an ear inefficient for reception of high-frequency airborne vibrations but well suited for bone-conducted hearing.

The triossicular mammalina middle ear transmits vibrations from the tympanic membrane (eardrum), supported by the ectotympanic bone, to the inner ear. Recognition that the mammalian auditory ossicles are transformed lower jaw and jaw suspensory elements of other gnathostomes represents a classic achievement in comparative biology[11]. The ear bones and the gnathic homologue are the ectotympanic (angular), malleus (articular plus prearticular), incus (quadrate) and stapes (hyomandibular).

The new specimens (V10777.1 and V10777.2, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) were recovered from the transitional Palaeocene–Eocene Bayan Ulan beds of Inner Mongolia, China. They are assignable to Lambdopsalis bulla, a specialized multituberculate, most cranial elements of which, apart from portions of the ossicular apparatus, have previously been described[5,12]. The new material demonstrates the presence and acoustic role of a well developed and, in every respect, 'typically mammalian' ectotympanic in this multituberculate (Fig. 1). This bone is completely detached from the lower jaw, lies horizontally against the base of the auditory region, and bears an internal groove for attachment of the tympanic membrane. Its position suggests a more medial and horizontal placement of the tympanic membrane than in non-mammalian cynodonts, where the angular bone forms part of the mandible. The body of the Lambdopsalis malleus is broad, and bears a long, robust anterior process (Fig. 1). Specimen V10777.2 demonstrates the Lambdopsalis malleus to be compound in structure, consisting of an anterior process (goniale, a prearticular derivative) plus the malleus proper (an articular derivative), precisely as in therians and monotremes[13,14]. The homology of the anterior process of the malleus and the prearticular is affirmed by the presence of a foramen for passage of the chorda tympani (Fig. 2), a branch of the facial nerve[11]. Detailed descriptions of the new material and a reconstruction of the Lambdopsalis middle ear are provided in Figs 1–3.

There is continuing controversy regarding the number of times that the mammalian triossicular system has evolved, recent estimates ranging from once[2,3,15] to as many as three times[5,6,16,17]. Of the numerous currently competing hypotheses of multituberculate affinities, four recent cladistic results are summarized in Fig. 4. As indicated below, ossicular evidence decidedly favours the alliance of multituberculate and monotreme, a finding consistent with the suggested single freeing of the ear bones from the dentary during the origin of the mammalian middle ear[2,3,11]. Otic similarities of Lambdopsalis and other mammals include: angular bone detached from the lower jaw, forming an ectotympanic enclosing the fully suspended tympanic membrane; articular and prearticular bones detached from the lower jaw, fusing to form malleus; and mutual spatial relationships between these elements and such basicranial landmarks as the chorda tympani maintained throughout this transformation. Even if the reduction of post-dentary bones in 'advanced' synapsids were prone to convergent evolution, as is often suggested[17], it seems unlikely that this adequately accounts for the numerous intricate resemblances of the mammalian sound-conducting system.

Regarding the relationship of multituberculates to other mammals, the following auditory features of Lambdopsalis lend support to the recently revised hypothesis of a monotreme-multituberculate pairing[10]. The ectotympanic is horizontally positioned, differing from a relatively vertical angular bone in near outgroups such as Morganucodon[18]; a horizontal ectotympanic occurring in certain therians is probably convergent[14]. The Lambdopsalis incus is simple and flat[12], contrasting with its more complicated form in non-mammalian cynodonts[19] and therians[13,16]. The incus lies dorsal to the malleus as in adult monotremes, a condition strikingly distinct from the anteroposterior relation of the malleus (articular) and incus (quadrate) in non-mammalian cynodonts[19] and therians[13,14,16]. The ectotympanic contacts the pterygoid anteromedially as in

FIG. 1 *a*, Ventral view of the left auditory region of *Lambdopsalis* (V10777.3); *b*, ventral view of partial left ectotympanic and articulated malleus (V10777.1), both in original life position; *c*, anterior (slightly lateral) view of V.10777.1; and *d*, dorsal view of a partial right malleus (V10777.2). c, Condyle; ct, foramen for the chorda tympani nerve; e, ectotympanic; er, epitympanic recess; fc, 'fenestra cochleae' (perilymphatic foramen); fi, incuidal fossa; fv, fenestra vestibuli; m, malleus; p, pterygoid. V.10777.2-3, from mature individuals, are slightly larger than V.10777.1, from a juvenile having an unerupted last molar (same scale for *b–d*). The posterior portion of the ectotympanic is missing and a crack separates its anterior and medial portions. The anterior portion of the ectotympanic underlaps the anterior process of the malleus; both bones lie nearly horizontally. The medial portion of the ectotympanic is crescentic and contacts the 'pterygoid' anteriorly. A groove for attachment of the tympanic membrane occupies the bone's inner edge. Unlike the thin, spring-like structure in most therians[13,16], the long anterior process of the malleus is robust and extends anteromedially. It is firmly connected, but not fused, to the ectotympanic. The malleus and ectotympanic are loosely attached to the basicranium and probably functioned as a single element acoustically. A foramen for passage of the chorda tympani nerve perforates the anterior process (broken dorsally in V10777.1) roughly midway along its length as in extant mammals[13,14]. The preserved portion of the transverse part (body) of the malleus bears a broad, concave ventral surface (*b*); dorsally this region forms a thick, triangular area which rests in the epitympanic recess (*c*, *d*). A fossa posterolateral to this thickened area is presumably for the incuidal articulation.
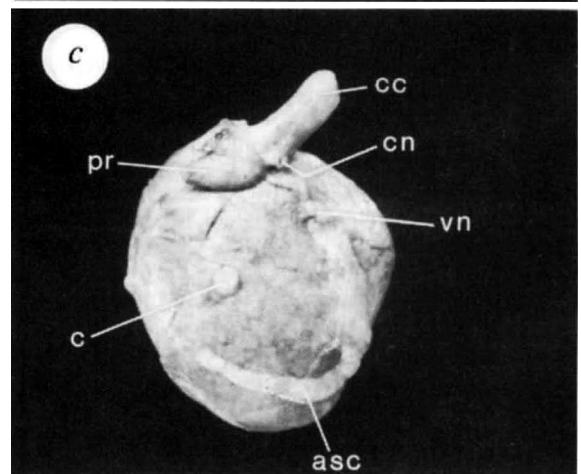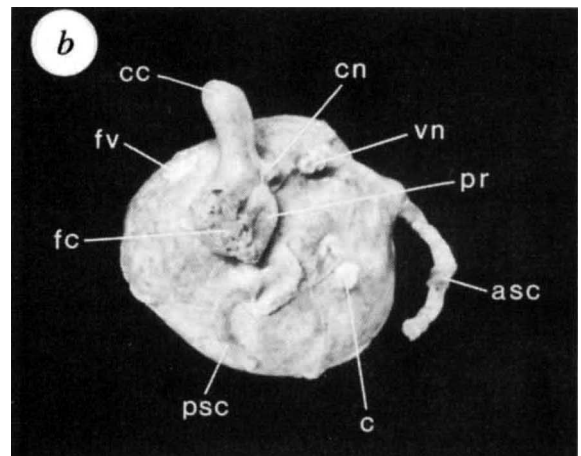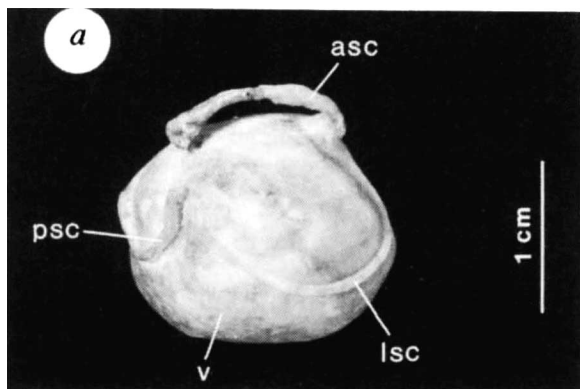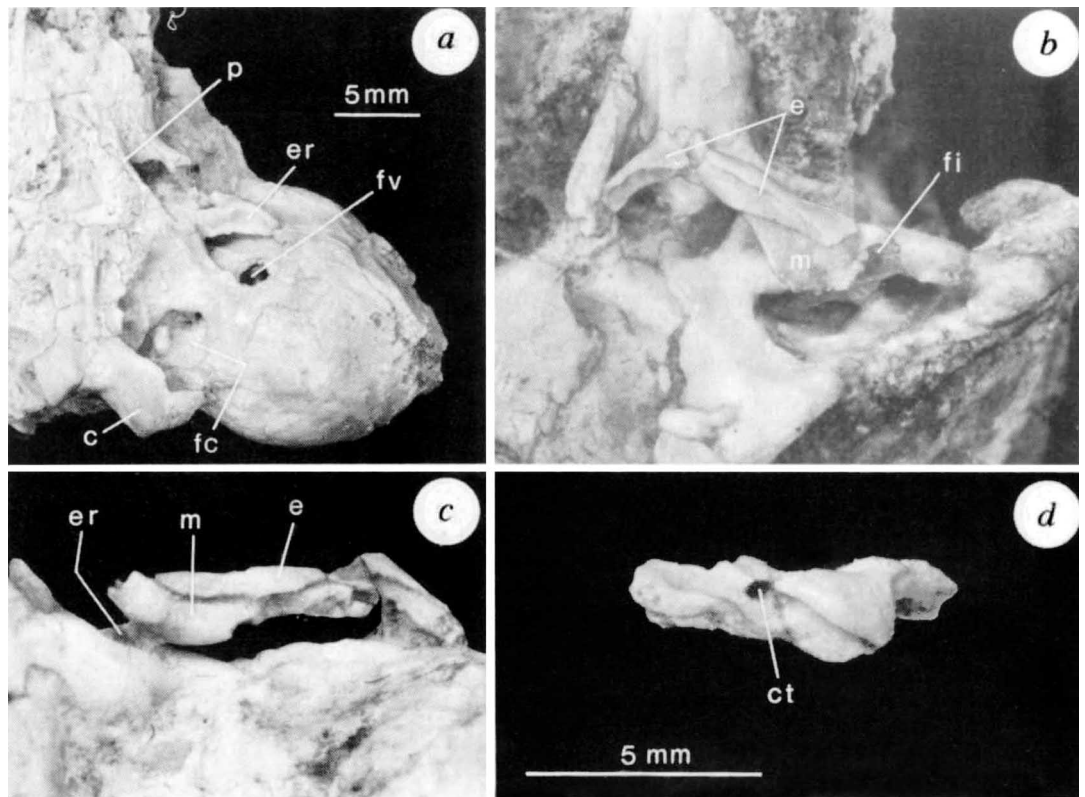

FIG. 2 Natural endocasts of the right inner ear of *Lambdopsalis*. *a*, Posterodorsal view (V10777.4); *b* and *c*, ventral and medial views (V10777.5). Abbreviations as for Fig. 1 plus: asc, anterior semicircular canal; c, crus commune; cc, cochlear canal; cn, cochlear nerve; lsc, lateral semicircular canal; pr, perilymphatic recess; psc, posterior semicircular canal; v, vestibule; vn, vestibular nerve. The semicircular canals are irregular in cross-section whereas the crus commune is circular. The lateral canals and most of the posterior canel are confluent with the vestibular space. The ovoid vestibule has an average volume of 785 mm³ (approximating the vestibule as an ellipsoid), remarkably, more than two orders of magnitude larger than in humans[24]. The vestibular nerve endocast subdivides, one branch entering the vestibule and the other leading dorsally to the ampulla of the anterior semicircular canal. The cochlear nerve passes the cochlear canal as a single bundle. The cochlear canal is 8.7 mm long from the posterior edge of the 'fenestra cochleae' to its tip. In ventral view its tubular form bends slightly laterally, the basal part being slightly narrower than the anterior part (except for the apical tip). No bony structures are preserved within it. The 'fenestra cochleae' is irregular in shape and is larger than the fenestra ovalis. Measurements (average diameter in mm; followed by number of specimens examined): semicircular canals (0.5 × 1.0; 7); loops of anterior, lateral and posterior semicircular canals (maximum 6.5, 9.1 and 5.2; 7); crus commune (1.1; 5); vestibule (10 × 15; 9); cochlear canal (maximum 1.9; 4); cochlear nerve bundle (0.68; 5); fenestra vestibuli (1.8 × 2.2; 23).
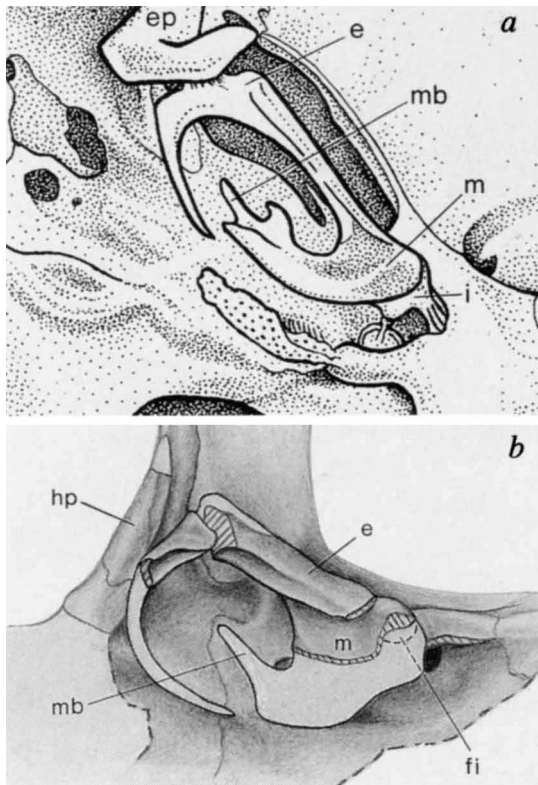
FIG. 3 Middle ears in ventral view of the platypus (a)[10] and *Lambdopsalis* (b) (anterior is up; not to scale). Reconstruction in b is based on specimens described herein and an illustration[12] plus a photograph of V7151.80 from D. Miao. Abbreviations as in Figs 2 and 3 plus: ep, 'ectopterygoid'; i, incus; mb, manubrium. The manubrium and part of the body of the malleus are preserved in V7151.80. Based on the new material reported here, it appears that the unusual posterolaterally directed manubrium of V7151.80 previously figured[12] is due to displacement. The new material thus shows the ossicular arrangement of *Lambdopsalis* to conform closely to the typical mammalian condition, particularly that seen in monotremes, where the manubrium is directed anteromedially. In addition to features mentioned in the text and Fig. 4 (Node 2), the ear of *Lambdopsalis* displays several primitive resemblances to monotremes: the ectotympanic is large and massive relative to, for instance, that in didelphid marsupials; the malleus is large and bears a robust anterior process; the broadly connected malleus and ectotympanic are loosely attached to the basicranium; the malleus lacks a protruding head; and the cochlear canal is uncoiled. The estimated maximum diameters of the tympanum (based on V10777.1, an immature individual) are 5.4 × 3.2 mm. The calculated primary transformer ratio[23] for transmitting sound vibrations to the inner ear is 3, an extremely low figure. There is no osseus trace of the external auditory meatus in the ear of *Lambdopsalis*, suggesting that it was cartilaginous and that its proximal end extended medially to the ventral side of the promontorium as in monotremes[27]. This contrasts with the condition in non-mammalian cynodonts where the external auditory meatus would, if present, have been lateral to the angular bone, i.e. lateral to the mandible[15].

monotremes (where it is variously termed 'ectopterygoid' or 'echidna pterygoid').

Many previous assessments of multituberculate relationships have, in our view, been unduly influenced by a reluctance to accept derivation of the peculiar multituberculate molar cusp pattern from a 'reversed triangle' arrangement. Inasmuch as taxa with such bizarrely specialized dentitions as *Shuotherium* are generally accepted as having a 'reversed-triangle' ancestry[20], and the multituberculate-like molar pattern of the megachiropteran bat *Harpyionycteris whiteheadi* certainly has a tribosphenic progenitor, the distinctive molar pattern of multituberculates seems
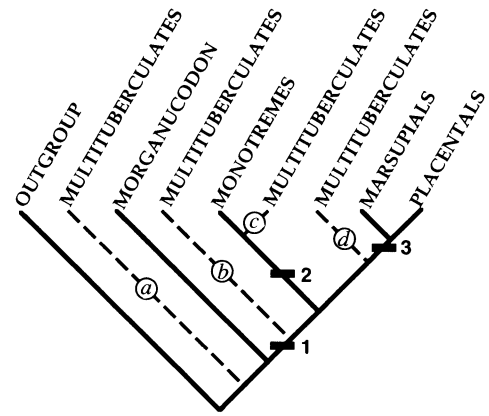

FIG. 4 Summary of previous cladistic proposals (a–d) concerning the phylogenetic affinities of multituberculates. Hypothesis a[6,28] is consistent with an assumed early divergence for multituberculates, but lacks supporting morphological evidence. Hypothesis d[7] is based on postcranial and to a lesser extent cranial information; reanalysis of the cranial component of this data set led to proposition of hypothesis b[8]. A recent treatment[29] also contradicts hypothesis d. Hypothesis c[2,4] was founded originally on a shared pattern of the braincase sidewall, a pattern later judged plesiomorphic[2,15], and still later as possibly advanced[9]. Hypotheses b, c and d are most parsimoniously interpreted in the context of a single origin of the triossicular system and derivation of the multituberculate molar pattern from a 'reversed triangle' ancestral condition, although these interpretations are sensitive to the currently insecure placement of certain fragmentary fossil forms such as *Kuehneotherium*. With the caveat that more data from other multituberculates is needed, synapomorphies of the auditory region supporting monophyly of indicated groups include: Node 1 (Mammalia[7]): angular detached from mandible, forming ectotympanic; suspension of tympanic membrane by ectotympanic near the basicranial region; medial extension of the external auditory meatus to ventral side of the promontorium; prearticular and articular detached from lower jaw and incorporated into middle ear as the malleus; manubrium mallei present and extends to the centre of tympanic membrane[15,16]; reduced quadrate (incus) losing the occlusal force from masticatory movement of the mandible[11,19]. Node 2 (Monotremata + Multituberculata): ectotympanic and malleus horizontally positioned[14]; ectotympanic contacts the 'pterygoid'; incus simple and flat[12]; incus dorsal to the malleus. Other features supporting this grouping are listed elsewhere[9,10]. Node 3 (Theria): anterior process of malleus thinned and reduced; cochlea coiled more than 360°; primary and secondary osseous spiral laminae developed; perilymphatic recess merging with scala tympani; radial pattern of cochlear nerve; and basal extension of basilar membrane[30].

no less plausibly derived from a 'reversed triangle' antecedent than from one in which molar cusps were arranged in a longitudinal row. In the absence of dental (or other) evidence convincingly demonstrating a remote phylogenetic placement of multituberculates, or placing some taxon retaining postdentary bones within the clade stemming from the most recent common ancestor of monotremes plus therians, there is little basis for judging the triosdicular chain to have originated more than once.

Functionally, the middle ear of *Lambdopsalis* was probably less sensitive to airborne sounds than in modern therians, judging from its close resemblance to monotremes[21,22]. The estimated area of the tympanic membrane in *Lambdopsalis* is small relative to that of the oval window; the resulting low primary transformer ratio[23](=3) suggests inefficient detection of airborne sounds. An inflated vestibule occurs to varying degrees among many multituberculates and is possibly associated with low-frequency hearing[5,24]. Increased separation of the stapedial footplate and cochlear base resulting from vestibular inflation dampens sensitivity to high-frequency vibrations given their rapid dissipation with distance from the stapedial footplate[25]. In addition, vestibular inflation probably enhances bone-conducted hearing; volumetric asymmetry between the scala tympani and

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.
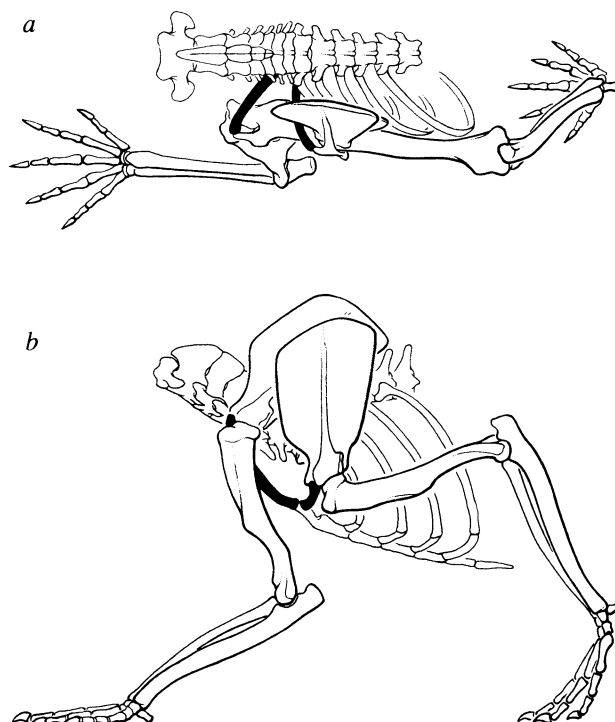

FIG. 1 *a, b*, Excursion of the left pectoral girdle and forelimb relative to the vertebral column and ribcage in a walking opossum (*Didelphis virginiana*) in dorsal (*a*) and lateral (*b*) views[1].

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