The ossified Meckel's cartilage and internal groove in Mesozoic mammaliaforms: implications to origin of the definitive mammalian middle ear

JIN MENG[1]*, YAOMING HU[1,2,3], YUANQING WANG[4] and CHUANKUI LI[4]

[1]*Division of Palaeontology, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024, USA.*

[2]*Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing, 100044, China.*

[3]*Biology Program (EEB), Graduate School and City College, City University of New York, NY 10016-4309, USA.*

[4]*Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing, 100044, China.*

The ossified Meckel's cartilage is described in detail from three adult individuals of two triconodont mammals, *Repenomamus* and *Gobiconodon*, which have been discovered in the Lower Cretaceous of Liaoning, China. A possible ossified Meckel's cartilage has also been recognized in the Early Cretaceous symmetrodont *Zhangheotherium* from Liaoning. The rod-like ossified Meckel's cartilage in *Repenomamus* bridges the dentary and the ear region of the cranium. Its shape and position are similar to those of Meckel's cartilage in prenatal and in some postnatal extant mammals. The ossified Meckel's cartilage may have functioned as an attachment site for the medial pterygoid muscle. These specimens provide direct evidence for the function of the internal groove which is commonly present in the dentary of early mammals and their relatives. The evidence weakens the hypothesis of multiple origins for the definitive mammalian middle ear. It supports the assumption that a persistent or ossified Meckel's cartilage has been present in adults of the common ancestor of mammals. The new evidence of *Repenomamus* does not support the model in which brain expansion and negative allometry of the auditory chain are primarily responsible for the detachment of ear ossicles in mammalian ontogeny and evolution. An alternative hypothesis is proposed which does not require brain expansion as the initial factor for the detachment of ear ossicles during mammalian evolution. © 2003 The Linnean Society of London. *Zoological Journal of the Linnean Society*, 2003, **138**, 431–448.

ADDITIONAL KEYWORDS: Cretaceous – evolution – Liaoning – Mammalia – ontogeny – triconodonts.

INTRODUCTION

A groove that extends longitudinally along the medial surface of the dentary is a common but puzzling feature present in many Mesozoic mammals and their relatives, known since the 19th century (Owen, 1871; Marsh, 1887; Osborn, 1888; Goodrich, 1894; Bensley, 1902). The groove varies in its position, shape and size. In some forms, more than one groove are present. Simpson (1928a) made the first systematic review of this structure based on the jaws of Mesozoic mammals

known at the time (Simpson, 1925a,b, 1928b, 1929). Because the function of the groove was uncertain, Simpson (1928a) employed 'internal groove' as a descriptive, unambiguous yet noncommittal term to denote the groove in question. In conclusion, Simpson (1928a) endorsed the view that the internal groove lodged a nerve or artery or both, probably resembling the mylohyoid groove of extant mammals (Owen, 1871; Osborn, 1888). Moreover, Simpson disfavoured Bensley's (1902) view that the groove was for the Meckel's cartilage.

Since Simpson's review (1928a, 1929), numerous additional Mesozoic mammals and their relatives have been discovered, such as *Kuehneotherium* (Ker-

mack, Kermack & Mussett, 1968), *Morganucodon* (Kermack, Mussett & Rigney, 1973, 1981), *Shuotherium* (Chow & Rich, 1982), *Gobiconodon* (Jenkins & Schaff, 1988; Rougier *et al*., 2001; Wang *et al*., 2001), *Haldanodon* (Lillegraven & Krusat, 1991), *Zhangheotherium* (Hu *et al*., 1997), *Ausktribosphenos* (Rich *et al*., 1997, 1999), *Hangjinia* (Godefroit & Guo, 1999), *Jeholodens* (Ji *et al*., 1999), *Repenomamus* (Li *et al*., 2000), and other triconodonts (Matsuoka, 2000). The lower jaws of many of these forms bear the internal groove, some of which are of morphologies which would have been unknown to Simpson (1928a), such as those in *Kuehneotherium* (Kermack *et al*., 1968), *Morganucodon* (Kermack *et al*., 1973), *Gobiconodon* (Jenkins & Schaff, 1988) and *Prokennalestes* (Kielan-Jaworowska & Dashzeveg, 1989).

Specimens of *Morganucodon* furnish the first critical evidence concerning the function of the internal groove (Kermack *et al*., 1973). *Morganucodon* is a mammaliaform (Rowe, 1988; McKenna & Bell, 1997) possessing jaw and middle ear structures which are closely comparable to those of early mammals. In *Morganucodon*, the postdentary bones are considerably reduced and, coeval with the primary jaw articulation between the quadrate and the articular, a dominant squamosal-dentary jaw articulation is developed. In *Morganucodon* a narrow groove, which was identified as the meckelian groove by Kermack *et al*. (1973), extends along the medial surface of the dentary. A long, slim pre-articular bone medially covers the groove. Based on evidence from *Morganucodon,* Kermack *et al*. (1973) advocated Bensley's (1902) view that the main function of the internal groove was to lodge a persistent Meckel's cartilage, although such an element was not actually preserved in specimens of *Morganucodon. Haldanodon* (Lillegraven & Krusat, 1991) provided additional evidence for the function of the internal groove. In many Mesozoic mammals (Rowe, 1988, 1993; McKenna & Bell, 1997), such as triconodonts and symmetrodonts, there is still no direct evidence of what the internal groove actually holds. Therefore, interpretation of its function remains controversial, which in turn hampers a hypothesis for the origin of the definitive mammalian middle ear (Allin & Hopson, 1992).

In all jawed vertebrates except mammals, the craniomandibular joint lies between the quadrate region of the palatoquadrate above, and the articular region of the Meckel's cartilage (or its replacement) below (Gaupp, 1913; Goodrich, 1930; Hopson, 1966; Allin, 1975; Maier, 1990; Allin & Hopson, 1992; Novacek, 1993; Zeller, 1993; Rowe, 1996a,b). Although the postdentary bones have probably functioned as a middle ear in nonmammalian synapsids, including *Morganucodon*, they are still attached to the dentary (Kermack *et al*., 1973, 1981; Allin, 1975; Allin & Hopson, 1992);

therefore, hearing and mastication are not completely separated. In mammals the craniomandibular joint lies between the squamosal and dentary, and the ear ossicles are fully suspended at the basicranial region as exclusively auditory apparatus. The transfer of accessory jaw elements to the cranium as strictly auditory structures is one of the central topics of comparative anatomy and the evolutionary biology of vertebrates (Gaupp, 1913; Goodrich, 1930; Hopson, 1966; Allin, 1975; Maier, 1990; Allin & Hopson, 1992; Novacek, 1993; Zeller, 1993; Rowe, 1996a,b). Although the homologies of these elements among jawed vertebrates have long been demonstrated by developmental studies of extant mammals (Reichert, 1837; Gaupp, 1913; Goodrich, 1930), fossil evidence on the critical transference from a condition seen in *Morganucodon* to that of mammals is sparse. The only evidence is the presence of the internal groove on the medial surface of the dentary bone (Allin & Hopson, 1992). The groove presumably lodges the anterior end of the postdentary unit (consisting of the articular, prearticular, angular and surangular) in some early mammals, such as *Peramus* and *Amphitherium* (Allin & Hopson, 1992). Alternative occupants of the internal groove include the splenial, as restored in dryolestids (Krebs, 1971), or a persisting Meckel's cartilage, as implied by developmental evidence of extant mammals (Bensley, 1902; Kuhn, 1971; Maier, 1987, 1990, 1993; Zeller, 1987, 1993). Interpretations of the function of the internal groove are important for a correct description of the origin of the definitive mammalian middle ear. For instance, because *Peramus* and *Amphitherium* are within the Trechnotheria of Mammalia (McKenna & Bell, 1997), interpretation of the presence of the postdentary unit in these taxa argues for a multiple origination of the definitive mammalian middle ear (Allin & Hopson, 1992). Therefore, any direct evidence of the function of the internal groove will be critical in an understanding of the evolution of the definitive mammalian middle ear.

Two Early Cretaceous triconodonts, *Repenomamus robustus* (Li *et al*., 2000; Wang *et al*., 2001) and a new species of *Gobiconodon* (Wang *et al*., 2001; Li *et al*., in press) were discovered in the lowest part of the Yixian Formation, Liaoning, north-western China, where many birds, dinosaurs and other mammals and vertebrates have recently been discovered (Wang *et al*., 1998, 1999). The two mammals, particularly *R. robustus,* are represented by well-preserved, three-dimensional specimens, including complete skulls and associated postcranials. The exceptional preservation of *R. robustus* was in sharp contrast to the squashed specimens of birds, dinosaurs and other mammals from the third member of the Yixian Formation. *R. robustus* is probably the largest Mesozoic mammal discovered to date. Partly because of its robustness,

many detail features of skulls, lower jaws and post-cranial skeletons were preserved, furnishing a wealth of data towards the morphologies of early mammals. One of the most interesting structures is a long, rod-like bone that is lodged anteriorly in the internal groove on the medial surface of the dentary and extends to the ventral side of the ear region posteriorly. This unusual, unexpected element was originally identified as the 'postdentary bar' by Li *et al*. (2000), but was later recognized as an ossified Meckel's cartilage (Wang *et al*., 2001). The element is found in both *Repenomamus* and *Gobiconodon*, and is best preserved in the former. With the benefit of these new materials, we recognized that the ossified Meckel's cartilage was also present in the symmetrodont *Zhangheotherium* (Hu *et al*., 1997) from Liaoning and also possibly in an Early Cretaceous triconodont from Japan (Matsuoka, 2000). The ossified Meckel's cartilage in *Repenomamus* was the first direct evidence for the function of the internal groove in Mesozoic mammals. With other cranial and mandibular features, this structure casts new light on the evolution of mammals in general, and that of the definitive mammalian middle ear in particular.

This study is a follow-up of a brief report on the ossified Meckel's cartilage of *Repenomamus* (Wang *et al*., 2001). Here we provide a more detailed description of the element, a briefly review on the internal groove and its function in Mesozoic mammaliaforms, and a discussion on the implications of the new evidence to the origin of the definitive mammalian middle ear.

MATERIAL AND METHODS

Two complete ossified Meckel's cartilages were found in two skulls of *Repenomamus robustus* (IVPP V12549 and IVPP V12728) (Figs 1–4). A partial ossified Meckel's cartilage came from a new species of *Gobiconodon* (IVPP V12585) (Wang *et al*., 2001; Li *et al*., 2003; Fig. 5). IVPP V12549, the holotype of *R. robustus*, is a skull with articulated lower jaws and associated partial skeleton. IVPP V12728 is also a skull with articulated lower jaws and partial postcranial skeleton. Three additional skulls with articulated lower jaws (V12613, V12732 and V13066), one skull without a lower jaw (V13067), a partial skull (V13065), and a partial lower jaw (V13068) are also in the collection. IVPP V12585 is a partial skull with articulated lower jaws. The skull of *Zhangheotherium* (IVPP V7466; Hu *et al.* 1997; Fig. 5) is squashed.

We followed Rowe (1988) and McKenna & Bell (1997) for the definitions and contents of Mammalia and Mammaliaformes, Wang *et al.* (2001) for the phylogenetic framework of the taxa relevant to the study, and Kielan-Jaworoska & Dashzeveg (1998) for the
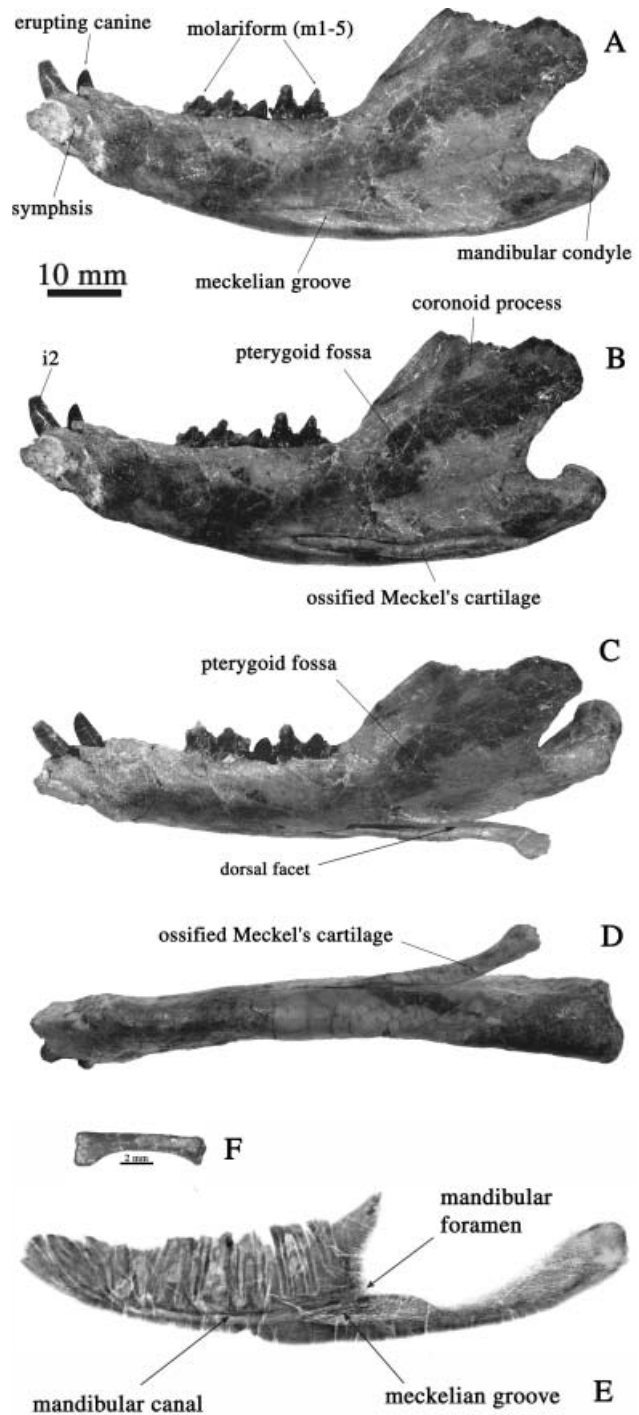
Figure 1. The right mandible and ossified Meckel's cartilage (OMC) of *Repenomamus* (holotype, IVPP V12549). (A & B) Medial views of the mandible with the OMC being removed in (A); (C) dorsomedial view; (D) ventral view; (E) radiographic image of the mandible; (F) a hyoid element from IVPP V12728. Modified from Wang *et al*. (2001).
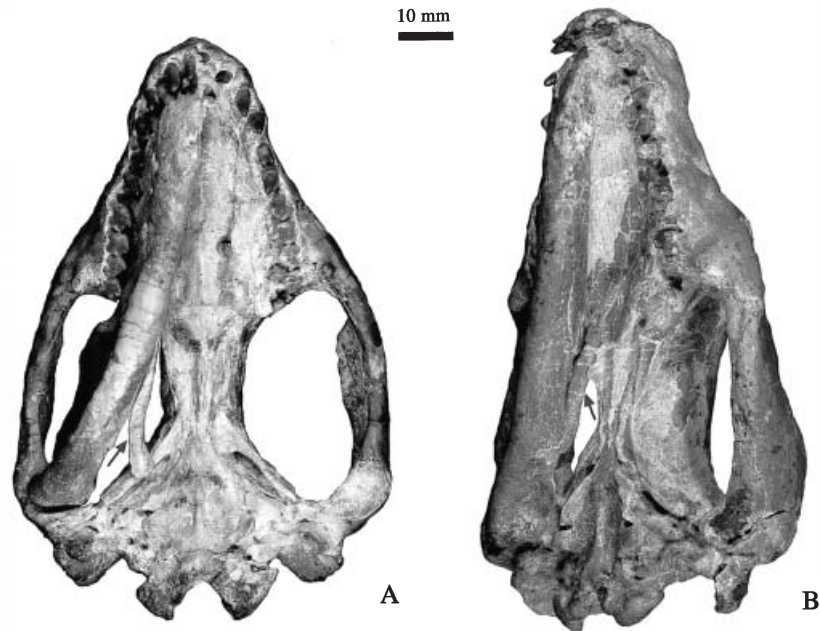
Figure 2. Skulls of *Repenomamus*. (A) Ventral view of IVPP V12549 (holotype), showing relationship of the ossified Meckel's cartilage (indicated by arrow) with the dentary and the ear region. (B) Ventromedial view of IVPP V12728, showing the displaced OMC (indicated by arrow). Modified from Wang *et al*. (2001).

usage of 'triconodonts' as an informal term. We adopted the definition of the definitive mammalian middle ear used by Allin & Hopson (1992), i.e. the configuration in which the angular, articular plus prearticular, and quadrate are strictly auditory structures, fully divorced from the feeding apparatus (and renamed the tympanic, malleus, and incus). The term 'ossified Meckel's cartilage' (OMC) is employed to denote the element described in the text, although the replacement of the cartilage is a more complex process than just 'ossified'. There is no simple term which would substitute for 'ossified Meckel's cartilage'. In addition, this term has been used elsewhere by anatomists (e.g. Zeller, 1993). Moreover, the replacement process of the cartilage is commonly described as 'ossified' or 'ossification' (Kuhn, 1987; Filan, 1991; Allin & Hopson, 1992; Clark & Smith, 1993; Zeller, 1993; Rowe, 1996a,b; Tomo, Ogita & Tomo, 1997). For convenience, Simpson's (1928a) 'internal groove' is used as a general, descriptive term for the groove(s) occurring on the medial surface of the dentary in the mammaliaform taxa selected for study. A committal term, such as the meckelian groove, will be specified where it is appropriate. We define the meckelian groove as the sulcus left by the developmental process of Meckel's cartilage, either in the shape of a distinct groove, a slit, or a combination of both; the sulcus may

or may not contain a persisting Meckel's cartilage in adults (see Discussion).

The institutional abbreviation IVPP: Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, is used throughout.

DESCRIPTION

The skull dimensions of the holotype of *Repenomamus* (V12549) are 108 mm long and 71 mm wide (Fig. 2A); the mandible is 82 mm long (Fig. 1). The bone identified as the ossified Meckel's cartilage (OMC) measures 33 mm long (Fig. 4A–D), although minute cracks running transversely through the bone may have slightly altered its length. The OMC is preserved in its original location, with its anterior portion lodged in the internal (meckelian) groove on the medial surface of the right dentary. During preparation, the OMC has been separated from the dentary. The element is rod-like and tapers anteriorly, with its anterior portion being transversely thin. Therefore, when the bone is lodged in the internal (meckelian) groove, the medial surface of the bone levels with the surface of the dentary. Its lateral surface, which contacts the dentary, is flat. Posterior to the mandibular (dental) foramen the OMC curves medially to depart from the dentary. A
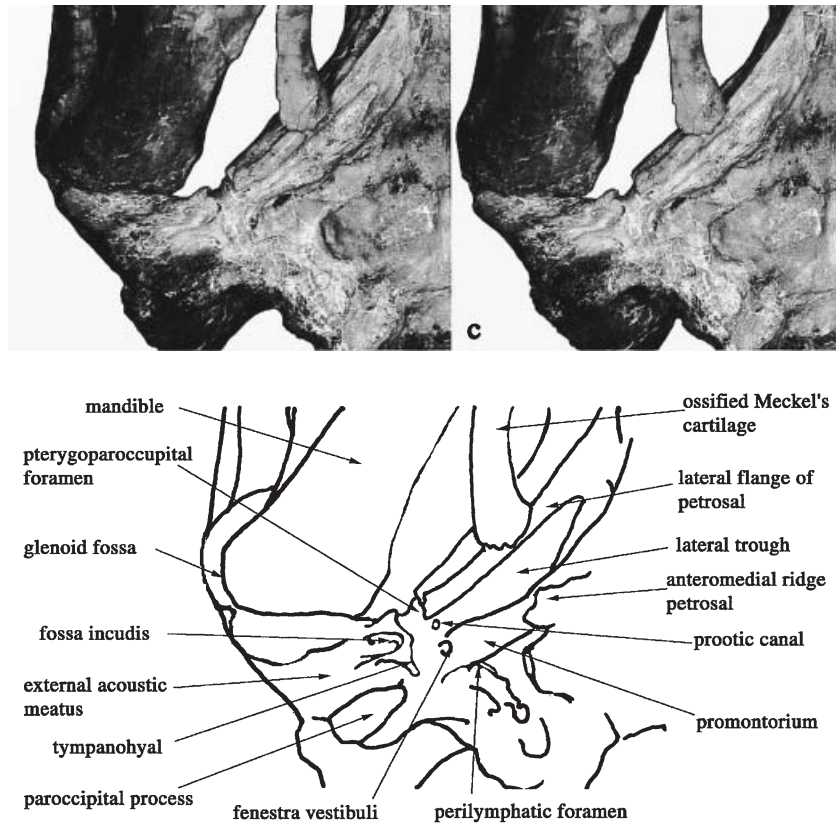
Figure 3. Stereophotos of the basicranial region of *Repenomamus* (holotype, IVPP V12549). Modified from Wang *et al.* (2001).
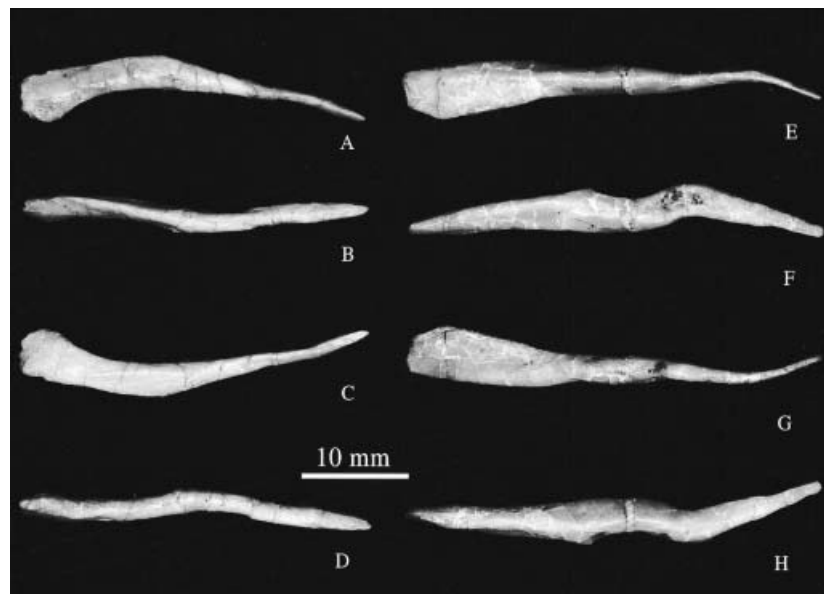
Figure 4. Ossified Meckel's cartilages (OMC) of *Repenomamus*. (A–D) Ventral, lateral, dorsal, and medial views of the OMC in IVPP V12549; (E–H) the same views of the OMC in IVPP V12728.
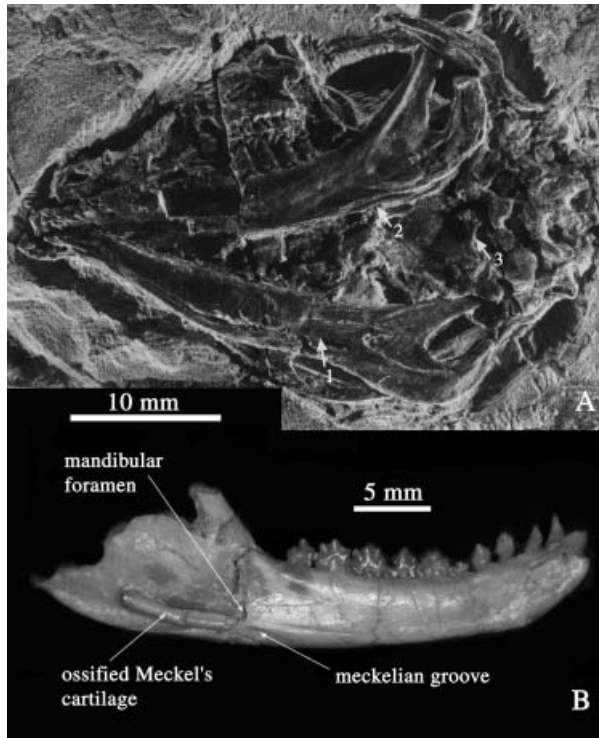
Figure 5. (A) The skull of *Zhangheotherium* (IVPP V7466). 1, Meckelian groove; 2, ossified Meckel's cartilage; 3, a hyoid element. (B) Medial view of the left mandible with partial ossified Meckel's cartilage of *Gobiconodon* (IVPP V12585).

significant segment of the OMC is free from the dentary and curves postero-medially. This curvature is unlikely to be caused by postmortem factors, such as shrinkage of muscle that could have attached to the element. There is no sign of any contact between the posterior portion of the OMC and the dentary along the ventral margin of the pterygoid fossa. In addition, the OMC is a robust element; if the dried muscle could have applied force to it, it should have pulled the OMC away from the dentary rather than bent it.

The dorsal side of this segment bears a flat facet, which was speculated to be for attachment of the medial pterygoid muscle (Wang *et al*., 2001; see below). The posterior section of the bone becomes more dorsoventrally compressed, or transversely expanded. The posterior end of the bone flares and is situated ventral to the lateral flange of the petrosal at the basicranial region. The rugosities on the dorsal side of the posterior end suggest its connection by connective tissue to the lateral flange.

V12728 is larger than V12549, with skull dimensions being 114 × 74.3 mm. The skull is slightly transversely distorted, so that the measured width is slightly narrower than life size. The mandible mea-

sures 93.3 mm long and the OMC, also from the right side, is about 40 mm (tip broken), which is longer and more robust than that of V12549. It was displaced during preservation and lies between the mandible and the skull (Fig. 2B). Although slightly distorted, this element is preserved in a better condition than that of V12549. The middle portion of the OMC shows a greater degree of curvature than that of V12549. At the most curved region of the element, the contact side with the dentary bears a small, rough-surfaced depression, which matches an uneven area in the posterior portion of the internal (meckelian) groove on the dentary.

The dorsal surface of the OMC of V12728 differs from that of V12549. A blunt knob with a rough surface on the dorsal side of the element marks the turning point of the element from a dorsoventrally deeper section to a transversely wider section. The dorsal surface posterior to the knob is a shallow, longitudinal groove which widens posteriorly. Judging by its length and curvature, the posterior end of the OMC would also extend to the ear region of the skull. Because of the distortion of the skull, a precise restoration of the element in relation to the dentary and skull is not possible. The OMC probably had some mobility in life for at least two reasons. First, the element has a loose contact with the dentary; it can therefore be easily detached. Second, in both V12549 and V12728, the anterior portion of the OMC is narrower than its host meckelian groove on the dentary, and some 'waggling space' appears to be present between the bones.

In addition to the OMC, a floating hyoid element is preserved at the basicraium of V12728, and preparation has removed this element (Fig. 1F). The hyoid element is much smaller than the OMC, measuring 8.3 mm in length. It is slightly curved, and flared at both ends. The rough surfaces on both its ends suggest its connection with the dorsal and ventral elements by ligament. The shape and size of this element is typical of a hyoid element, such as the ceratohyal, in extant mammals. Because it was preserved as an isolated element, its relationship with other cranial structures cannot be determined. A possible hyoid element is present in the skull of *Zhangheotherium* (Fig. 5A).

The meckelian groove is distinct in all lower jaws of the *Repenomamus*. It lies along the lower part of the dentary. The posterior portion of the groove that holds the OMC is broad and has a rounded base. Its dorsal edge ends posteriorly ventral to the mandibular foramen, whereas its ventral edge extends further posteriorly, terminating at the ridge that ventrally bounds the pterygoid fossa. The anterior tip of the groove continues anteriorly as a fine slit, which varies in length among the lower jaws. The longest slit is seen in V12613 and extends to the symphysis. Following our definition, both the portion that lodges the OMC and

the narrow slit are considered as parts of the meckelian groove. The slit follows the course of the mandibular canal contained within the dentary. As revealed by radiographic imaging of the lower jaws (V12549; Fig. 1E), the mandibular (inferior dental) canal, through which the dentary inferior dental nerves and artery pass, is ventral to the long roots of the check teeth and extends from the mandibular (inferior dental) foramen to the symphysis. The canal is narrow anteriorly and slightly broadens posteriorly. At the position where the anterior tip of the OMC is situated, the mandibular canal turns slightly dorsally and continues posteriorly to merge at the mandibular (inferior dental) foramen. In the radiographic images, the meckelian groove appears to have continuity anteriorly with the mandibular canal (Fig. 1E), although the groove is separated from the canal by bone.

The OMC in V12585, which represents a new species of *Gobiconodon* (Li *et al*., 2003) is incomplete. Its posterior end and anterior tip were broken, but the bulk of the element is still attached to the posterior end of the meckelian groove (Fig. 5B). It is similar to, but proportionally thicker than, that of *Repenomamus*. The preserved portion is pushed laterally towards the surface of the pterygoid fossa. Similar to that of *Repenomamus*, the anterior portion of the bone is transversely compressed, whereas the suspended segment is rod-like. Different from *Repenomamus*, there are two grooves present on the medial surface of the dentary of V12585. A short, broader groove that lodges the OMC is ventral to the mandibular foramen. The length of the groove indicates that the anterior portion of the OMC is proportionally shorter than that of *Repenomamus*. The second groove is dorsal to the first, separated from the latter by a fine ridge. It is narrow and well defined, and extends from the mandibular foramen to a level below the last premolariform tooth. The double-grooved condition in other triconodonts has been described by Simpson (1928a).

In light of the evidence from *Repenomamus*, an OMC is recognized in *Zhangheotherium*, a symmetrodont from the third member of the Yixian Formation (Fig. 5A). Along the ventral edge of the left dentary, a thin bone is present, but was previously not identified (Hu *et al*., 1997). Because the skull of *Zhangheotherium* (IVPP V7466) was squashed, it was impossible to separate the dentary from the thin bone. From what is exposed, the bone is narrower anteriorly than posteriorly, and extends from m3 to the anterior side of the promontorium of the petrosal. The shape and size of this bone are similar to those of the OMC in *Repenomamus*. Therefore, we consider it a displaced OMC. On the same specimen, a hyoid element lies adjacent to the OMC; it is thinner and shorter than the latter. The medial side of the right dentary of *Zhanghetherium* is exposed, showing a distinct internal groove. The groove is similar to that of *Repenomamus* in its position and shape, but extends more anteriorly along the dentary. The size and shape of the groove match the bone identified as the OMC.

An OMC is also possibly preserved in a triconodont from the early Cretaceous Kuwajima Formation of Japan (Matsuoka, 2000, fig. 61-1). It appears that the element is in its original position, although its anterior tip and posterior portion were broken.

IDENTIFICATION

In close relatives of mammals, two sets of accessory elements are attached to the dentary: the paradentary bones (coronoid and splenial) and postdentary bones (the endochondral articular and dermal prearticular, angular and surangular) (Allin, 1975; Allin & Hopson, 1992). The paradentary bones are plate-like, abutting the medial side of the lower jaw, and have no relationship with the basicranium (Allin, 1975; Kermack *et al*., 1973; Allin & Hopson, 1992). Within the postdentary bones, the articular bears a retroarticular process, which is the homologue of the manubrium of the mammalian malleus, and extends posteriorly to articulate with the quadrate. The surangular also extends posteriorly to articulate either with the squamosal or with the quadrate (Allin, 1975; Kermack *et al*., 1973; Allin & Hopson, 1992). The angular has a reflected lamina that primitively supports the anterior margin of the tympanic membrane of the mandibular ear in close relatives of mammals, such as *Morganucodon* (Allin, 1975; Allin & Hopson, 1992). In mammals, the angular becomes the tympanic bone that holds the tympanic membrane. The prearticular in *Morganucodon* is straight and is posteriorly fused to the articular. In mammals, the dermal prearticular forms the anterior process of the malleus. Because there is no other scar on the dentary, it can be inferred that all postdentary bones in *Repenomamus* have been detached from the dentary. It is also clear that the detached elements are small, as reflected by the structures in the ear region. The dimensions of the fenestra vestibuli in V12549 are 1.1×1.8 mm, which suggests a small footplate of the stapes. The distance of the fenestra vestibuli to the medial edge of the fossa incudis is 3.5 mm. The dimensions of the fossa incudis are 2.1×3 mm. The distance of the fenestra vestibuli to the medial edge of the glenoid fossa is 6.4 mm. These measurements indicate that, in relation to the sizes of the skull and the mandible, the ear ossicles of *Repenomamus* must have been small. Given these conditions, the bone in question is too big to be the prearticular. Thus, the shape and size of the bone in question and its relationship to the dentary and cranium indicate that it is not any of the postdentary bones.

One reviewer of our earlier paper (Wang *et al*., 2001) suggested that the bone in question is an ossified ceratohyal, a hyoid element, and thus has the origin of the second visceral arch. We believe this view is unlikely. In mammals, the dorsal extremity of the hyoid arch, the tympanohyal, is fused to the basicranial (Fig. 3). Ventrally, the tympanohyal is connected to the basihyal by a chain of ossicles, including the stylohyal, epihyal and ceratohyal. The basihyal is further ventrally connected with the thyrohyal (3rd visceral arch), which caudally attaches to the larynx. In no mammals, or their relatives, is a hyoid element lodged in the mandible. The shape and size of the bone in question does not match any of the hyoid elements of mammals. Instead, the floating element identified as a hyoid element in the basicranial region of V12728 (Fig. 1F) shows typical mammalian hyoid size and morphology.

The bone in question is most probably the ossified middle portion of Meckel's cartilage. Its shape and relationship to the cranium and dentary are closely comparable to those of Meckel's cartilage in prenatal and some postnatal extant mammals (Kuhn, 1971; Zeller, 1987, 1993; Maier, 1990; Clark & Smith, 1993). It is the Meckel's cartilage, not the prearticular or any other postdentary element, that is rod-like, bridges the dentary and the ear region, and remains as the last connection of the lower jaw with the ear region during the ontogeny of extant mammals. In nest young marsupials (Bensley, 1902; Maier, 1987, 1993; Clark & Smith, 1993), monotremes (Kuhn, 1971; Zeller, 1989, 1993) and eutherians (Zeller, 1987; Tomo *et al*., 1997), it is a common pattern to find that the anterior portion of Meckel's cartilage lies in a medial groove of the dentary, whereas the posterior end extends to the ear region and forms the anlage of the malleus. Even in fully grown juveniles of living mammals, Meckel's cartilage can still exist between the dentary and ear region. Kuhn (1987: 11) has observed that 'in serial sections of the head of a fully grown, although juvenile, *Micropotamogale lamottei*, Meckel's cartilage is still complete from dentale to the auditory bulla.' The relationship of the bone in question with the mandibular canal and foramen is also closely similar to that of Meckel's cartilage in extant mammals. For instance, in a sectioned foetus of *Macropus* (Bensley, 1902) Meckel's cartilage was separated from the dental nerve and artery at the mandibular (dental) foramen. The nerve and artery entered the foramen and course anteriorly within the dentary to the symphysis, but are separated from the cartilage by a bony strip.

The persistence of Meckel's cartilage in adults of the common ancestor of mammals has been inferred (Bensley, 1902; Kermack *et al*., 1973; Zeller, 1993; Rougier, Wible & Novacek, 1996). E.F. Allin (pers. comm.) pointed out that there is strong evidence for the persistence of Meckel's cartilage in nonmammalian synapsids, not just in the internal (meckelian) groove of the dentary, but between the posterior end of this groove and the quadrate bone. This is shown by a well-defined groove bounded laterally by the lateral portion of the surangular, medially by the prearticular, and ventrally by the angular, as is seen in *Probainognathus*. A similar pattern is also present in *Morganucodon* (Kermack *et al*., 1973). Thus, not only does embryological evidence demonstrate a continuity of Meckel's cartilage with its ossified posterior extremity (the malleus); fossil evidence also supports this continuity, even in mature individuals. The ossified Meckel's cartilage of *Repenomamus* is an exaggeration of a pre-existing feature, enlarged in length and diameter as well as being ossified.

DISCUSSION

IMPLICATIONS OF *REPENOMAMUS*

Developmental studies of living mammals have revealed that the posterior portion of Meckel's cartilage forms the anlage of the malleus and that the middle portion of the cartilage degenerates in the later stages of ontogeny. The sheath of the middle portion of the cartilage becomes the sphenomandibular ligament (pterygomandibular in monotremes) or the anterior ligament of the malleus (Gaupp, 1913; Goodrich, 1930; Allin & Hopson, 1992). By its relationship with the ear region, the OMC in *Repenomamus* and *Gobiconodon* provides evidence for a relationship of Meckel's cartilage with the definitive mammalian middle ear in early mammals, which is otherwise only inferred from embryological evidence of living mammals. The *Repenomamus* specimens showed that, while the anlage of the malleus is reduced, or posteriorly shifted, to form a small malleus, a significant middle segment of Meckel's cartilage persists and is even ossified in adults of some early mammals and close relatives. This fact supports the assumption that a persisting and possibly ossified Meckel's cartilage connecting the malleus to the lower jaw was present in the common ancestor of mammals (Zeller, 1993). The OMC in *Repenomamus* probably remains in its early ontogenetic position, as in extant mammals in which the cartilage extends from the dentary to the ventral side of the ear region. A similar condition is possibly present in other early mammals, such as triconodontids and symmetrodontids, in which an internal groove similar to the meckelian groove of *Repenomamus* is present.

The function of the ossified Meckel's cartilage in adults of *Repenomamus* and *Gobiconodon* is unclear. Because a facet exists on the dorsal side of the ossified Meckel's cartilage in *Repenomamus* (Fig. 1F), we have

speculated that a portion of the medial pterygoid muscle originates on the pterygoid region of the skull and inserts to the ossified Meckel's cartilage. There is enough space between the pterygoid area of the skull and the dorsal facet of the OMC to allow the muscle to work. This speculation was based on a comparison with marsupials and multituberculates, in which the medial pterygoid inserts to the inflected angular process in marsupials (Sánchez-Villagra & Smith, 1997), or to the pterygoid shelf in multituberculates (Gambaryan & Kielan-Jaworowska, 1995). As in other triconodonts and in symmetrodonts, the mandible of *Repenomamus* lacks the angular process or pterygoid shelf. Although a ridge defining the ventral border of the pterygoid fossa is present in the mandible of *Repenomamus*, it is a much weaker structure than is the inflected angular process in marsupials or the pterygoid shelf in multituberculates. The position and shape of the OMC in relation to the dentary and the pterygoid fossa in *Repenomamus* resembles the inflected angular process or the pterygoid shelf; it may have functioned as an additional site for the partial insertion of the medial pterygoid muscle. This condition may represent an intermediate condition during the evolutionary shift of the jaw-elevating muscle insertion from the postdentary bones to the dentary, a trend documented in the transition from cynodonts to mammals (Crompton, 1963; Barghusen, 1968; Barghusen & Hopson, 1970).

Rugosities on the posterior end of the OMC in *Repenomamus* suggest a connection by ligament to the lateral flange in life. This contact functions as a hinge that operates in concert with that of the dentary-squamosal. Although the hinge is anterior to that of the dentary-squamosal, and therefore not coaxial, the ossified cartilage can still rotate with the dentary as the latter was depressed and elevated because of the possible mobility at the contact of the dentary and the OMC.

The ear ossicles in early mammals other than therians are poorly documented in the fossil record. The presence of these elements are known only in multituberculates (Miao & Lillegraven, 1986; Miao, 1988; Meng & Wyss, 1995; Rougier et al., 1996), but are inferred in other groups, such as triconodonts (Allin & Hopson, 1992), based on jaw and cranial morphologies. For most Mesozoic mammals and their close relatives, however, jaw and skull materials are often fragmentary, which obstructs inference of the shape and size of the ear ossicles and their relationships with surrounding structures.

Although actual ear ossicles are not preserved in *Repenomamus*, well preserved skulls and mandibles provide a reliable basis for inference of the ear ossicles. Identification of the OMC leads to the conclusion that *Repenomamus* and *Gobiconodon* have a definitive

mammalian middle ear because the dentary of the two taxa lacks other scars for the postdentary bones. In addition, lack of the angular process, and therefore absence of the angular gap, suggests a separation of the middle ear from the dentary. For the same reason, the definitive mammalian middle ear is probably present in *Zhangheotherium*. A similar conclusion has been reached for triconodontids (Allin & Hopson, 1992; Rowe, 1996a,b), in which the ear ossicles have not been recovered. Given the phylogenetic relationship and other ear structures, such as the fossa incudis and fenestra vestibuli, which are comparable to those of other species that have the ear ossicles (or their equivalents), we have no reason to believe that ear ossicles are phylogenetically absent in *Repenomamus* and *Gobiconodon*.

Compared to those of close relatives of mammals, such as *Morganucodon*, *Probainognathus* and *Pachygenelus* (Hopson, 1966; Allin, 1975; Allin & Hopson, 1992; Luo & Crompton, 1994), the fossa incudis and fenestra vestibuli, and distance between these structures, as well as the general size of the tympanic region of *Repenomamus* are relatively small. In addition, the ectotympanic and malleus of *Repenomamus* were probably inclined, similarly to those of monotremes (Kuhn, 1971; Zeller, 1987, 1993), multituberculates (Meng & Wyss, 1995; Rougier et al., 1996) and those in early ontogenetic stage of therians (Starck, 1967). The inclined orientation of these elements is also suggested by the tilted fenestra vestibuli of *Repenomamus*, based on a roughly parallel relationship between the fenestra vestibuli and ectotympanic in living mammals (Rougier et al., 1996). Moreover, there is no supporting structure for a vertically orientated ectotympanic. The lateral flange, crista parotica and anteromedial ridge of the petrosal can only support an inclined ectotympanic and malleus.

The fossa incudis is immediately medial to the secondary craniomandibular joint (dentary-squamosal) in *Repenomamus* and *Zhangheotherium*. This relationship shows that in early mammals the secondary craniomandibular joint is lateral to the primary joint (malleo-incudal = quadrate-articular), not anterior to the primary joint as was shown in the ontogenesis of living mammals (Reichert, 1837; Gaupp, 1913; Zeller, 1989, 1993; Maier, 1990). It also shows that in early mammals the ear ossicles are medial, not posterior, as in extant mammals (Rowe, 1996a,b), to the secondary craniomandibular joint. The ear structure of *Repenomamus* probably represents an intermediate condition between the mandibular ear of nonmammalian synapsids, such as *Morganucodon* (Kermack et al., 1981), and the definitive mammalian middle ear of mammals in which the ear ossicles are widely separated from the secondary craniomandibular joint and

lie behind intervening secondary auditory structures (Rowe, 1996a,b).

Coexisting with the detached ear ossicles in *Repenomamus* are other auditory and feeding features. These include an elongated promontorium, a distinct external auditory meatus, an expanded glenoid fossa and mandibular condyle, enlarged pterygoid fossa, and broad masseteric fossa. These features can be attributed to the more efficient hearing of air-borne sound, and to more powerful mastication, respectively.

With the new data from *Repenomamus* and the new *Gobiconodon*, a phylogenetic analysis has been attempted (Wang *et al*., 2001). The cladogram (Fig. 6) is the consensus (tree length = 275; CI = 0.589; RI = 0.706) of four equally most parsimonious trees that are obtained by branch-and-bound searches using PAUP* 4.0 b8 (Swofford, 2000) based on a data set consisting of 112 craniodental characters across 20 taxa. The phylogeny is largely in keeping with other recent phylogenetic hypotheses of mammals and their

relatives (Rowe, 1988; Rougier *et al*., 1996; Hu *et al*., 1997; Ji *et al*., 1999; Luo, Crompton & Sun, 2001). Within the phylogeny, acquisition of the definitive mammalian middle ear in *Repenomamus* and *Gobiconodon* is consistent with the prediction that triconodontids have fully detached ear ossicles (Allin & Hopson, 1992). Whether the definitive mammalian middle ear is a synapomorphy for Mammalia, which probably occurred in the middle Jurassic, based on fossil records, or it is shared by Mammalia and *Hadrocodium* and thus evolved in the early Jurassic (Luo *et al*., 2001), depends on the interpretation of *Hadrocodium* (Wang *et al*., 2001; see below).

FUNCTION OF THE INTERNAL GROOVE

Simpson (1928a) noted that the internal groove is present in three of the four Jurassic groups: Triconodonta, Symmetrodonta and Pantotheria, and is absent in Multituberculata. Although the phylogenies
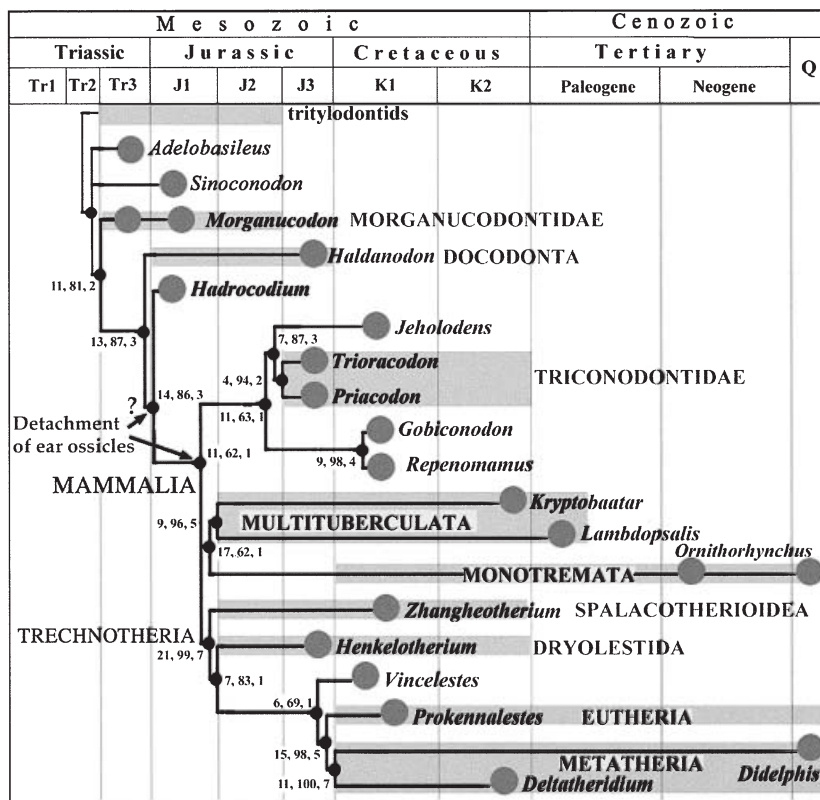
Figure 6. Phylogenetic relationships and distributions of main mammaliaform groups. Search options include: all characters unordered, equally weighted, accelerated transformation, multistate as uncertainty, rooting at tritylodontids, and monophyletic in-group. Numbers at each node represent assigned branch length, bootstrapping value, and Bremer supporting index. Bootstrapping value is obtained by 1000 replications of heuristic searches. Grey dots represent occurrences of genera (McKenna & Bell, 1997) used in the phylogenetic analyses. Grey bars are distributions of higher taxa (McKenna & Bell, 1997) represented by the genera. Character list, sources of data and detailed tree descriptions can be found in Wang *et al*. (2001).

and classifications of these groups have been changed significantly since then (McKenna & Bell, 1997), Simpson's observation still holds. Based on his observation of jaws of Mesozoic mammals and their relatives known at the time, Simpson (1928a) listed several possible functions for the internal groove, including: (1) lodged a reduced splenial bone; (2) fortuitous owing to irregular ossification or other causes; (3) lodged the Meckelian cartilage; (4) muscle attachment; (5) lodged a nerve or artery or both, such as the mylohyoid of later mammals; and (6) involved two of the above. Simpson (1928a) favoured the view that the groove lodged a nerve or artery or both (Owen, 1871; Osborn, 1888). This view was followed by Jenkins & Schaff (1988) and partly by Krebs (1971), who thought that the groove in dryolestoids held the mylohyoid artery and nerve, as well as a persisting Meckel's cartilage. Krebs also reconstructed the splenial to cover the posterior part of the groove in the mandible of dryolestoids. On the other hand, Simpson (1928a) disfavoured Bensley's (1902) view that the groove(s) is for the meckelian cartilage. Simpson (1928a: 466) stated: 'Since the internal groove is often very strong, regular and definite even in the most senile animals, it could only mean that, if due to the Meckelian cartilage, this must have persisted throughout life. But the fact that these are known to be true mammals, with the mammalian ear structure and jaw articulation, makes such persistence almost impossible of acceptance.' It is unclear why Simpson considered that a persistent Meckel's cartilage was inconsistent with the presence of the definitive mammalian middle ear.

Evidence from *Repenomamus* demonstrates that a persistent or even ossified Meckel's cartilage can coexist with the definitive mammalian middle ear in adults of early mammals, which supports the view of Bensley (1902). In *Repenomamus*, the posterior portion of the groove is relatively short but quite broad. The anterior portion is a fine slit resembling that of dryolestoids. It is probable that the slit represents the trace left by the anterior Meckel's cartilage as the dentary wraps over the cartilage during the ontogeny. Such a process is demonstrated in the ontogeny of extant mammals, such as *Rattus*, in which three-dimensional features of the developmental process are observed (Tomo *et al.*, 1997). A similarly narrow meckelian groove is present in immature specimens of extant mammals (Bensley, 1902). The slit is not an impression of a persisting Meckel's cartilage; instead, it is related to, or resulting from, the development of Meckel's cartilage. Thus, the meckelian groove is considered here to be the sulcus left by the developmental process of Meckel's cartilage, either in the shape of a distinct groove or a slit or a combination of both; the sulcus may or may not contain a persisting Meckel's cartilage in adults.

Although an ossified Meckel's cartilage was not actually preserved in *Morganucodon*, Kermack *et al.* (1973: 129) clearly favoured Bensley's view by stating that 'Bensley (1902) was right when he suggested that the main function of the groove was to lodge a persistent Meckel's cartilage.' The internal groove of *Morganucodon* is similar to that of *Repenomamus* in its relationship to the mandibular foramen (inferior dental foramen in *Morganucodon* (Kermack *et al.*, 1973). In both forms, the grooves are on the lower part of the dentary. In *Repenomamus*, the dentary is deeper and more robust, and the groove is relatively short. In *Morganucodon*, the dentary is shallower and the middle part of the internal groove runs along the ventral edge of the dentary. The internal groove in *Morganucodon* continues posteriorly with the postdentary trough (Kermack *et al.*, 1973).

Because the internal groove in triconodonts is similar to that of *Repenomamus*, we believe that, in most triconodonts, it also lodges a persistent Meckel's cartilage. In symmetrodonts the dentary shows different conditions (Cassiliano & Clemens, 1979). For those that have the internal groove, an OMC should be considered as a main occupant. This is further evidenced by the specimen of *Zhangheotherium* in which the OMC is probably present. For dryolestoids that possess the internal groove, it is relatively narrow and long. As Simpson (1928a) had already noted, this kind of groove appears too narrow to hold any bony element. However, the posterior part of the internal groove in some dryolestoids shows expansion (Krebs, 1971; Martin, 1999) and may have been covered by the splenial, as was reconstructed by Krebs (1971). An alternative interpretation is that the posterior part of the groove in those dryolestoids was occupied by a persisting Meckel's cartilage.

It has also been postulated that the internal groove in *Peramus* and *Amphitherium* accommodates the anterior portion of the postdentary unit (Allin & Hopson, 1992). Because *Peramus* and *Amphitherium* are in the Trechnotheria (McKenna & Bell, 1997), the interpretation of the postdentary unit in these taxa argues for multiple origins of the definitive mammalian middle ear (Allin & Hopson, 1992). Evidence from *Repenomamus* demonstrated that in early mammals, including *Peramus* and *Amphitherium*, a persistent Meckel's cartilage should be considered as the primary occupant for the groove in question. Given that potential, it follows that *Peramus* and *Amphitherium* may have developed the definitive mammalian middle ear.

The OMC in *Repenomamus* provides an alternative interpretation for the scar on the medial surface of the dentary in *Chronoperates paradoxus*, a presumably mammal-like reptile from the Palaeocene (Fox, Youzwyshyn & Kraus, 1992a). The scar was considered (Fox *et al.* 1992a: 234) for lodging 'one or more postdentary

bones, including the splenial.' However, the conclusion was controversial (Fox, Youzwyshyn & Kraus, 1992b; Sue, 1992). With the evidence from *Repenomamus*, a persisting Meckel's cartilage may be considered to occupy the scar on the medial surface of the dentary in *Chronoperate*.

Although an ossified Meckel's cartilage may be the main structure occupying the internal groove in many early mammals, such as *Peramus* and *Amphitherium*, it may not be the sole element filling the internal groove, or grooves, in all those species. As Simpson (1928a) noted, the groove in the Jurassic forms has a dual cause or was due to a double structure, and it often branches posteriorly. This condition exists on the lower jaw of *Gobiconodon* (V12585). Even for *Repenomamus*, the mylohyoid artery and nerve that supply the mouth floor may have extended along the suture between the ossified Meckel's cartilage and the dentary, or on the medial surface of the ossified Meckel's cartilage, as has been discussed previously (Bensley, 1902; Simpson, 1928a). Therefore, viewed within the phylogenetic framework, the evidence weakens, but cannot sufficiently reject, the hypothesis of multiple origins of the definitive mammalian middle ear (Allin & Hopson, 1992). In any case, however, the OMC as an important factor responsible for the formation of the internal groove is substantiated.

DETACHMENT OF EAR OSSICLES

Brain-expansion model

The most uncertain issue in the evolution of the definitive mammalian middle ear is how the postdentary unit became detached from the dentary, and translocated to the basicranium as ear ossicles (Hopson, 1966; Allin, 1975, 1986; Maier, 1990; Allin & Hopson, 1992; Zeller, 1993; Rowe, 1996a,b). One model suggests that a heterochronic increase in the rate and duration of brain development may have been the driving force behind the origin of the definitive mammalian middle ear (Rowe, 1996a,b). According to this model, there is a negative allometry of growth of the auditory chain in relation to that of the brain. Ear ossicles approach their mature size during early stages of development while still attached to the lower jaw. The brain continues to grow for a much longer time during postnatal development. As the circumference of the growing brain expands, the distance between the secondary craniomandibular joint and the ear region, represented by the landmark fenestra vestibuli, is widened and the ear ossicles are torn away from the mandible and carried backwards to their adult position behind the jaw. This mechanism was thought to account for detachment of the ear ossicles in both mammalian ontogeny and phylogeny (Rowe, 1996a,b).

However, the brain morphology and its relationship with the ear in early mammals, such as triconodonts, has not been well documented. The shape and relative size of an endocast of *Triconodon* (Simpson, 1927) were thought to be similar to didelphid endocasts, which was used as an example supporting the brain-expansion model (Rowe, 1996b). Compared to those of nonmammal cynodonts, such as *Probainognathus*, the brain of *Triconodon* is only slightly widened, and the widening is primarily at the forebrain (Jerison, 1973; Ulinski, 1986). The topographic relationship of the brain with the ear and jaw joint is uncertain because of the fragmentary preservation of *Triconodon* material. It remains unclear how the expanded brain in *Triconodon* is related to the detachment of the ear ossicles.

The new evidence from *Repenomamus* challenges the brain-expansion model in several aspects. *Repenomamus* has a narrow braincase, as revealed by X-ray images and by direct observation of a broken skull (Wang *et al*., 2001; Fig. 2). Using the methods of Luo *et al*. (2001), the width of the 'brain vault' of *Repenomamus* (IVPP V12547) measures 28 mm across the maximum distance between the squamosal-parietal sutures. The actual brain vault of *Repenomamus* is narrower because the wall of the braincase is 3.7 mm thick. The width between the secondary craniomandibular joints is 60 mm (between the midpoints of the glenoid fossae). Taking 28 mm as the width of the 'brain vault', the maximum ratio of the estimated brain vault to the skull width in V12549 is 49% (a similar ratio is obtained from V12728), which is smaller than those of *Sinoconodon* and *Morganucodon* in which the postdentary unit is attached to the dentary (Kermack *et al*., 1981; Crompton & Sun, 1985; Luo *et al*., 2001). This indicates that detachment of the ear ossicles is not necessarily associated with expansion of the brain during mammalian evolution.

It may be argued that during early ontogeny, *Repenomamus* would have had a proportionally larger brain that might have applied traction to the postdentary elements. Assuming this is true, it still does not explain why the ear ossicles (as indicated by the position of fossa incudis) is so close to the jaw joint in the adult skull. One has to assume that in the early ontogeny of *Repenomamus* the brain expansion increased the distance between the ear region and the secondary craniomandibular joint, so that the ossicles could be detached. In a later stage of development, the distance between the ear and the jaw was somehow closed up. There is no evidence to support this developmental process.

The association of the ear ossicles to the mandible in the early ontogeny of extant mammals takes place by virtue of the horizontal limb of the ectotympanic and, more substantially, of Meckel's cartilage (Goodrich,

1930; Maier, 1987, 1990; Filan, 1991; Clark & Smith, 1993; Rowe, 1996a,b; Sánchez-Villagra *et al.*, 2002). It is universally accepted that the separation of the malleus from the mandible is due to the degeneration and resorption of Meckel's cartilage. The same is at least partly true for the ectotympanic. In early stages of ontogeny in *Monodelphis*, the horizontal limb of the ectotympanic extends anteriorly between Meckel's cartilage and the posterior border of the mandible. As observed by Clark & Smith (1993: 132): 'During the 3rd week (14–21 days) the anterior process of the ectotympanic is resorbed in *M. domestica*, and although the ectotympanic is still in proximity to the mandible, after loss of the anterior process its primary structural association is with the middle ear.' These studies show that ontogenetic factors other than brain expansion must also be attributable to the ossicle detachment.

The presence of the OMC in *Repenomamus* suggests that the separation of the malleus from the rest of the OMC may not be caused by brain expansion. If the posterolateral expansion of the brain pulls the ossicles away from the mandible, it is difficult to explain why the posterior portion of the OMC in *Repenomamus* bends medially. In addition, if the posterolateral expansion of the brain pulls the middle ear ossicles away from the mandible in the early stage of ontogeny of *Repenomamus*, a gap should be present between the posterior end of the OMC and the malleus. The position of the posterior end of the OMC at the ear region suggests that there is no significant distance between the two structures.

Rowe (1996a,b) used the fenestra vestibuli as the landmark in calculating the distance between the ear and the secondary craniomandibular joint. We believe the fossa incudis (epitympanic recess, quadrate notch) is probably a better reference point for measuring the distance for early mammals and their relatives, although it may be difficult to observe in embryonic specimens of extant species. This is because the distance between the fossa incudis and the secondary craniomandibular joint is less affected by the sizes and orientations of the ear ossicles, particularly the stapes (see below). In *Repenomamus* the fossa incudis (or epitympanic recess), which reflects the position of the incus and the incudomalleolar articulation, is immediately medial to the secondary craniomandibular joint between the mandibular condyle and the squamosal. The distance between the joint and the fossa incudis is proportionally similar to, or even smaller than, the space between the quadrate recess and the secondary craniomandibular joint in *Morganucodon* (Kermack *et al.*, 1981; Luo & Crompton, 1994; Luo *et al.*, 2001). It should be noted that the quadrate notch (fossa incudis) and the quadrate in *Morganucodon* were reconstructed to be closer to the glenoid fossa than to the fenestra vestibuli in Kermack *et al.*

(1981), whereas the reverse is true in Luo & Crompton (1994). The ear morphology of *Repenomamus* appears more consistent with the interpretation of Kermack *et al.* (1981). Even using the fenestra vestibuli as a reference point, the distance between the ear and the secondary craniomandibular joint of *Repenomamus* is still proportionally similar to or smaller than, that of *Morganucodon*. These facts show that the separation of the postdentary bones from the dentary does not require an increase in the distance between the ear and the mandible.

Moreover, the fossa incudis and fenestra vestibuli in adult *Repenomamus* and *Zhangheotherium* are medial to the jaw joint. This indicates that shifting of the ear ossicles backwards to the mature position behind the jaw in extant mammals (Rowe, 1996a,b) is not necessarily a factor for the detachment of the ossicles in early mammals. In other mammals in which the ear ossicles are detached, such as multituberculates (Miao & Lillegraven, 1985; Miao, 1988; Meng & Wyss, 1995; Rougier *et al.*, 1996) and monotremes, the ossicles are similarly medial to the jaw joint.

In a study of *Hadrocodium* Luo *et al.* (2001) concluded that 'The concurrence of the expanded brain vault and the separation of the middle ear from the mandible in *Hadrocodium* is consistent with the observed correlation of the peramorphic growth of brain and basicranium to the separation of the middle ear bones from the mandible during development.' This conclusion contradicts our study on the role played by the brain expansion in detachment of the ear ossicles during mammalian evolution. The type specimen of *Hadrocodium* (IVPP V8275) was originally regarded as a juvenile *Morganucodon* (Crompton & Luo, 1993), but is now thought to be an adult, or a subadult, of a distinctive taxon (Luo *et al.*, 2001). Luo *et al.* (2001) considered that the postdentary unit of *Hadrocodium* was already detached from the dentary. In our earlier work (Wang *et al.*, 2001) we have questioned whether the type specimen of *Hadrocodium* is a postsuckling juvenile. We still consider it an adequate question. When many potential juvenile features of *Hadrocodium*, such as its small size, erupting first upper postcanine tooth, only two molars, a slender mandible, a proportionally large space between m2 and the coronoid process, a large promontorium, and a large brain vault, are considered in combination, the possibility that V8275 is a postsuckling juvenile cannot be unambiguously excluded.

Nonetheless, assuming that V8275 was an adult or subadult individual, we found that expansion of the brain vault in *Hadrocodium* does not seem to support the brain-expansion model. As illustrated by Luo *et al.* (2001: fig. 2), the epitympanic recess in *Hadrocodiun* is medial, not posterior, to the secondary craniomandibular joint. More importantly, the distance between

the epitympanic recess and the secondary craniomandibular joint in *Hadrocodium* is proportionally smaller than the space between the quadrate recess and the jaw joint in *Morganucodon* (Luo & Crompton, 1994). This contradicts the assumption that expansion of the brain increases the distance between the ear and the mandible and thus pulls off the ear ossicles from the dentary (Rowe, 1996a,b; Luo *et al*., 2001).

Luo *et al*. (2001) observed that in nonmammalian mammaliaforms the fenestra vestibuli is medially aligned with the secondary craniomandibular joint and occipital condyles, and that in *Hadrocodium* the zygoma swings anteriorly from the cranial moiety of the squamosal, and the jaw joint is positioned anterior to the level of the fenestra vestibuli and to occipital condyles, correlating with the expanded brain vault. The observation raises two issues. First, the change of the relative positions between the ear and the jaw joint may be attributable to an anterior shift of the gleaned fossa as a result of masticatory modification. Such a shift is a common condition within extant mammals, but has not been considered in the brain-expansion model. Second, the more posteriorly located fenestra vestibuli certainly reflects a positional change of the stapes in relation to the incus, but it does not necessarily reflect positional changes between the incus and malleus or between the malleus and the mandible. The epitympanic recess, or the fossa incudis, is a better reference point for indicating the relationship of the mandible and the detached ossicles. In this regard, the epitympanic recess of *Hadrocodium* is medially aligned with the jaw joint and shows little change compared to the condition in *Morganucodon*, except that the two structures are closer to each other in *Hadrocodium*, as noted above.

Although the sizes of the ear ossicles were not discussed in the brain-expansion model (Rowe, 1996a,b), we think it a critical factor for the detachment of ear ossicles from the dentary. It makes sense, only when the sizes of the ossicles are considered, in discussing the role of the changing distance between the ear and the mandible for the detachment of the ossicles during mammalian evolution. The fossil record documents a gradual reduction in the postdentary bones, the quadrate, quadratojugal and stapes to minute ossicles. This trend leads to a refined auditory apparatus which is sensitive to high frequency sounds (Allin, 1975, 1986; Bramble, 1978; Crompton & Parker, 1978; Kemp, 1982; Kermack & Kermack, 1984; Rowe, 1996a,b). As Allin (1975: 403) concluded: 'Auditory efficiency, and sensitivity to higher sound frequencies, were enhanced by diminution and loosening of the postdentary elements and quadrate.' Loosening of the postdentary elements is associated with a reduction of these elements. This is probably because a reduction in the elements reduces their contact area with the

dentary bone and therefore weakens the tie between these elements.

Another relevant issue is the orientation of the ear ossicles. The angular (ectotympanic) is still attached to the lower jaw in a steep position in *Morganucodon* (Kermack *et al*., 1973), whereas in the early ontogeny of mammals and many adults of living mammals, the tympanic is in an inclined or horizontal position (Starck, 1967). Therefore, the positional change of the tympanic must have taken place during the evolution of early mammals (Carroll, 1988; Maier, 1993). Because of its close relationship with the ectotympanic, the position of the malleus has probably undergone a similar change with the tympanic. The brain-expansion model (Rowe, 1996a,b) does not explain why the malleus and tympanic are inclined, or even horizontally positioned, in multituberculates, monotremes and some eutherians. Ontogenetic studies have shown that the ear ossicles may have been convergently transferred into a similar, almost horizontal position by lateral and ventral displacement of the sidewall of the braincase and of the otic capsule, because of independent brain expansions in monotremes and therians (Kuhn & Zeller, 1987; Zeller, 1993). In adult marsupials, the tympanic lies in a more vertical position. Maier (1990, 1993) believed that a later expansion of the promontory and tympanic cavity secondarily relocates the tympanic ring in such a steeper position. Both Maier (1990, 1993) and Zeller (1993) realized that if the horizontal position of the tympanic ring present in monotremes and most eutherians were a primitive mammalian condition (Van Kampen, 1905; Gaupp, 1913; Van der Klaauw, 1931; Starck, 1967), then it contradicts to the fact that the progenitor of the ectotympanic, the angular, is attached to the lower jaw in a relatively vertical position. Maier (1990; see below) thus proposed that the development of marsupials may serve as a morphological model explaining the detachment of the ear ossicles.

The marsupial model
Marsupials have a different developmental pattern of the ear from those of monotremes and eutherians (Maier, 1987, 1990; Sánchez-Villagra & Smith, 1997), mainly because the medially inflected angular process has a close relationship with the tympanic ring. This relationship was believed to be characteristic of all marsupials examined (Sánchez-Villagra & Smith, 1997). As observed by Maier (1987, 1990, 1993), at birth the dentary of *Monodephis* is in a relatively upright position, and the developing tympanic and gonial are medially attached to it. Due to rapid postnatal expansion of the brain the upper part of the dentary is shifted laterally so that the dentary with the

adjacent tympanicum gets into a more and more oblique position. At about the time of lip opening and first teeth eruption, the dentary grow rapidly and begins to erect to a more vertical position, which is probably due to the requirements of chewing, whereas the angular process remains in contact with the bullar region and thus becomes medially inflected. Meanwhile, the tympanicum and the goniale have become fixed by ligaments to bony processes of the petrosal and alisphenoid, and therefore remain attached to the basicranium. Thus, the ossicles are decoupled from the lower jaw. There is evidence that movements of the jaw itself contribute to the detachment of the ossicles. As was stated by Maier (1993: 175): 'This decoupling may possibly be directly caused by the increasingly mobile dentary, because some destruction of the connective tissues between the angular process and the tympanic ring can be observed at this time.' Later expansion of the promontory and tympanic cavity secondarily relocates the tympanic ring into a steeper position.

Although both authors used *Monodephis domestica* as the model animal, Maier's (1990, 1993) hypothesis differs from that of Rowe (1996a,b) in several aspects. First, the main influence of the brain expansion to the ear region is to force the dentary and ossicles to an oblique position during the early ontogeny. Second, the distance between the dentary and ear region is not an issue for detachment of the ear ossicles. Third, the ear ossicles are not 'torn off' from the dentary by brain expansion; instead, they are 'fixed' by connective tissue to basicranial region while the dentary erects to a more vertical position. Fourth, the jaw movement probably contributes to the detachment of the ear ossicles from the dentary. Finally, the steep position of the tympanic in adults is secondarily developed.

Maier's model confronts two problems as it is applied to early mammals. First, in *Repenomamus* and several other taxa, such as triconodontids, amphilestids, gobiconodontids and symmetrodonts, an angular process is absent. The marsupial model does not seem readily suitable to those early taxa. Second, and more importantly, although we believe the ear ossicles of *Repenomamus* are in an oblique position, it may not be caused by brain expansion, because the brain of *Repenomamus* is narrow. In fact, as we have shown above, it is proportionally narrower than those of *Morganucodon* and *Sinoconodon* in which the postdentary bones are still attached to the dentary.

An alternative hypothesis

Evidence from *Repenomamus* allows the formulation of an alternative hypothesis for the origin of the definitive mammalian middle ear, which is partly based on ontogenetic evidence from marsupials (Maier, 1987,

1990). During the evolution of synapsids the postdentary unit is reduced and loosened to enhance hearing of high-frequency airborne sounds (Allin, 1975), whereas the dentary was enlarged for the attachment of more muscle to facilitate efficient mastication (Crompton, 1963; Barghusen & Hopson, 1970; Allin & Hopson, 1992). The position of the OMC in *Repenomamus* suggests that the common ancestor of mammals probably had a developmental pattern in which Meckel's cartilage extended from the dentary to the ear region. As shown by embryonic evidence of extant mammals, Meckel's cartilage is the earliest element to be developed in the lower jaw. The dermal dentary bone occurs on the lateral side of the cartilage and gradually expands to wrap over Meckel's cartilage, while the latter continues to reduce its size (Gaupp, 1913; Goodrich, 1930; Zeller, 1987, 1993; Filan, 1991; Clark & Smith, 1993; Tomo *et al*., 1997; Sánchez-Villagra *et al*., 2002). Because of the close relationship of the dentary to Meckel's cartilage, the position of the OMC in *Repenomamus* suggests that the embryonic dentary is probably in a horizontal orientation in early stages of development and reorients to a more vertical position in the later stage, as in marsupial development (Maier, 1987, 1990). The reduction of the postdentary bones increasingly weakened their tie to the dentary until a critical point was reached that the dentary, while erecting to a more vertical position during ontogeny, no longer seized the postdentary bones. The postdentary bones were moored at the basicranium by connective tissue as exclusively auditory ossicles. Meckel's cartilage was bent when the dentary erected, as in the case of *Repenomamus*. A weak contact between the reduced ossicles and the dentary is probably amplified by the fact that during early ontogeny, the dentary ossification is initially confined to the anterior portion of the lower jaw and progresses posteriorly during ontogeny, as in marsupials (Clark & Smith, 1993). Movements of the jaw itself may have contributed to the detachment of the ossicles. Thus, modifications in both feeding and hearing apparatuses toward efficient functions have led to the decoupling of the postdentary unit and the dentary. Expansion of the brain, along with changes in the otic capsule, probably causes further displacements of the ear ossicles to a position which iseither vertical, horizontal, or posteriorly distant from the secondary craniomandibular joint in more advanced mammals.

Unlike the marsupial model of Maier (1990), this hypothesis does not require brain-expansion as the initial factor to force the dentary and ear ossicles to an inclined position. It intimates that in the common ancestor of mammals the ear ossicles were probably positioned in an inclined position in early ontogeny, and that the inclined position of the ectotympanic and malleus in adult mammals is a retention of the embry-

ological condition of ancestral forms. It therefore implies a paedomorphic phenomenon during the evolution of the definitive mammalian middle ear.

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