EARLIEST KNOWN MAMMALIAN STAPES FROM AN EARLY CRETACEOUS EUTRICONODONTAN MAMMAL AND IMPLICATIONS FOR EVOLUTION OF MAMMALIAN MIDDLE EAR

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The earliest known mammalian stapes with unequivocal morphology from an Early Cretaceous eutriconodontan, *Chaoyangodens lii*, is described. The stapes is roughly rectangular in dorsal view with parallel crura and equal width on both the distal and proximal ends. The stapes has a large stapedial foramen and a prominent process that is interpreted as for insertion of the stapedius muscle (PISM). The PISM is homologized with the proximal end of the interhyal, instead of the dorsal process of the sauropsid extrastapes; the latter is fused to the crista parotica of the otic capsule as the tympanohyal in mammals. The morphology of the stapes is probably characteristic of the transitional mammalian middle ear and supports the notion that the rod-like, perforated stapes with a broad end-on contact with the incus is a primitive stapes condition for mammals. During the evolution of mammalian middle ear, the distal end of the stapes and the PISM reduced the size, along with reduction of other ear ossicles. Because the stapedius muscle is absent in monotremes, the columelliform-imperforate stapes of monotremes probably lacks the homologue of the PISM.

Key words: Stapes, eutriconodontan, mammal, Cretaceous, middle ear, evolution.

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INTRODUCTION

The definitive mammalian middle ear (DMME) (Allin and Hopson 1992) in mammals (Rowe 1988) differs from other extant tetrapods in having a unique middle ear that consists of multiple ossicles. In contrast, the middle ear of non-mammalian amniotes has one ossicle, the stapes (or columella auris). The evolution of the DMME has been a subject that has attracted enormous attention since at least Reichert (1837) and Gaupp (1908, 1913) and still remains as an interesting topic in the study of mammalian evolution. Incorporation of the malleus-incus complex into the middle ear during the early evolution of mammals resulted in an increased bandwidth of hearing and was thus a great biological advantage in mammals (Fleischer 1978). Significant progress has been made recently in documenting middle ear morphologies in Mesozoic mammals, including the ossified Meckel's cartilage, the malleus (= the articular and prearticular), incus (= quadrate) and ectotympanic (= angular) (Wang *et al.* 2001; Meng *et al.* 2003, 2011; Luo *et al.* 2007; Ji *et al.* 2009; Luo 2011). Based on these recent discoveries, the transitional mammalian middle ear (TMME) has been hypothesized as an intermediate stage between the mandibular middle ear, as represented in *Morganucodon* (Kermack *et al.* 1973, 1981), and the DMME in all extant mammals (Allin and Hopson 1992).

In addition to new discoveries made in paleontology, evolution of the mammalian middle ear has also continued to attract considerable attention from developmental and molecular studies that focus on the homology and gene expression of middle ear ossicles and related structures (Maier 1990; Zeller 1993; Mallo 1998, 2001, 2003; Sánchez-Villagra *et al.* 2002; Tucker *et al.* 2004; Wilson and Tucker 2004; O'Gorman 2005; Takechi and Kuratani 2010; Anthwal *et al.* 2013; Gillis *et al.* 2013; Kitazawa *et al.* 2015). More interestingly, paleontological findings and results of developmental biology converge in revealing not only the homology of the middle ear ossicles but also development of structural details of the ossicles, such as the manubrium as a neomorphic outgrowth of the malleus (Allin and Hopson 1992; Clack and Allin 2004; Meng *et al.* 2011; Anthwal *et al.* 2013).

However, the aforementioned developmental and paleontological studies have focused primarily on the ear ossicles that are transformed mandibular elements of non-mammalian cynodonts. In contrast, the stapes of Mesozoic mammals remains little known and less investigated, as already pointed out by Novacek and Wyss (1986). Although the stapes was discovered in the mid 16th century (Mudry 2013), its homology is still a controversial subject in developmental and evolutionary biology. The stapes has been known as the most conservative element of the middle ear ossicles, with its essential form and ontogeny being traceable across vertebrates (Goodrich 1930; Eaton 1939; Romer 1941; Westoll 1943; Parrington 1949, 1955, 1979; Tumarkin 1968; Fleischer 1978; Lombard and Bolt 1979; Novacek and Wyss 1986; Allin and Hopson 1992; Clack and Allin 2004). As Eaton (1939, p. 117) concluded: "The crossopterygian hyomandibular bone, evolving into the tetrapod stapes, retains its original morphological relations largely unchanged, even to mammals." In addition, the articulation between the stapes and incus in mammals represents the quadrate-hyomandibular joint that was present in ancestral amniotes (Kitazawa *et al.* 2015).

The stapes is rarely preserved in early mammals because of its small size and fragility. Among known Mesozoic mammals, there is one nearly complete stapes reported from a Late Cretaceous eutherian (Archibald 1979). Fragments of the stapes were reported from the Late Cretaceous multituberculate *Kryptobaatar* (Rougier *et al.* 1996a) and *Chulsanbaatar* (Hurum *et al.* 1996) and from Early Cretaceous eutriconodonts (Luo *et al.* 2007; Meng *et al.* 2011). Except for the stapes from a Late Cretaceous eutherian (Archibald 1979), the unambiguous morphology of the stapes remains poorly known in Mesozoic mammals and most of their close relatives, such as *Haldanodon* (Lillegraven and Krusat 1991; Ruf *et al.* 2013), *Morganucodon* (Kermack *et al.* 1981), and *Sinoconodon* (Crompton and Luo 1993). As yet, there is no convincing evidence of the stapes known from eutriconodontans.

Because of the scant fossil record, the ancestral condition of the stapes in mammals and transformation of the mammalian stapes during evolution of the mammalian middle ear has remained contradictory (Novacek and Wyss 1986; Meng 1992). It is posited that the rod-like, perforated stapes is the most likely ground plan for derivation of the mammalian stapes and that it probably persisted in "triconodonts" because of its common occurrence in cynodonts and other tetrapods (Novacek and Wyss 1986). Here we report the stapes with unequivocal morphology from the Early Cretaceous eutriconodontan *Chaoyangodens lii* Hou *et* Meng, 2014. It is the earliest known mammalian stapes, given current phylogenetic placements of the eutriconodontans within Mammalia (Luo *et al.* 2002, 2007; Kielan-Jaworowska *et al.* 2004; Rowe *et al.* 2008; Yuan *et al.* 2013; Zheng *et al.* 2013; Bi *et al.* 2014; Krause *et al.* 2014). The morphology of the stapes supports the notion that the rod-like, perforated stapes is a primitive condition for mammals. It provides new evidence about the stapes morphologies during the evolution of the mammalian middle ear, from the mandibular middle ear to the TMME and then to DMME. It also raises the issue on the homology of the process for insertion of the stapedius muscle in therians, a feature to which little attention has been paid.

Institutional abbreviations. — JTZ, Ji-Zan-Tang Paleontological Museum, Chaoyang, Liaoning Province, China; MGL, Museu Geológico de Lisboa, Lisbon, Portugal.

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MATERIAL AND METHODS

The holotype specimen of *Chaoyangodens lii* Hou *et* Meng, 2014 (JZT005-2010) is a skeleton from the lacustrine beds of the Yixian Formation at the Dawangzhangzi locality, Lingyuan, western Liaoning, China (Hou and Meng 2014, p. 548, fig. 1). The age of the strata has been generally considered as Early Cretaceous, but the radiometric dates vary from 122.2 Ma (Smith *et al.* 1995; Wang *et al.* 1999) to 124.6 Ma (Swisher *et al.* 1999, 2002). Other mammals from this locality include the multituberculate *Sinobaatar lingyuanensis* Hu *et* Wang, 2002, the trechnotherian *Akidolestes cifellii* Li *et* Luo, 2006, the metatherian *Sinodelphys szalayi* Luo *et al.*, 2003, and the eutherian *Eomaia scansoria* Ji *et al.*, 2002.

The skeletal specimen is preserved as a split slab of laminated siltstone, with the skeleton being primarily in slab A. The dorsal side of the skull is exposed and the right stapes is preserved in close approximation to the basicranial region of the skull and posterior to the petrosal (Fig. 1). No other ear ossicle has been detected from the crushed specimen. The miniscule stapes is mainly in slab A (Fig. $1B_1$), with its impression in slab B (Fig. $1B_2$).

In referring to Mammalia, we adopt the crown mammal concept (Rowe 1988), noting that different definition for mammals have also been used (Kielan-Jaworowska *et al.* 2004). Measurements were made using a microscope equipped with a reticule etched with divisions of 0.01 mm.

DESCRIPTION

The holotype is crushed so that detailed morphology of the skull is difficult to obtain, but the skull length measures 33.7 mm from the rostrum tip to the posterior edge of the occipital condyles (Hou and Meng 2014, fig. 1). The ossified Meckel's cartilage (OMC) is preserved in anatomical position on the medial side of each mandible (Fig. 1A). As in other eutriconodonts, including *Repenomamus* (Wang *et al.* 2001; Meng *et al.* 2003), *Gobiconodon* (Li *et al.* 2003), *Yanoconodon* (Luo *et al.* 2007), and *Liaoconodon* (Meng *et al.* 2011), the OMC is rod-like with a blunt posterior end and tapers anteriorly; its anterior portion is loosely lodged in the Meckelian groove on the medial surface of the dentary.

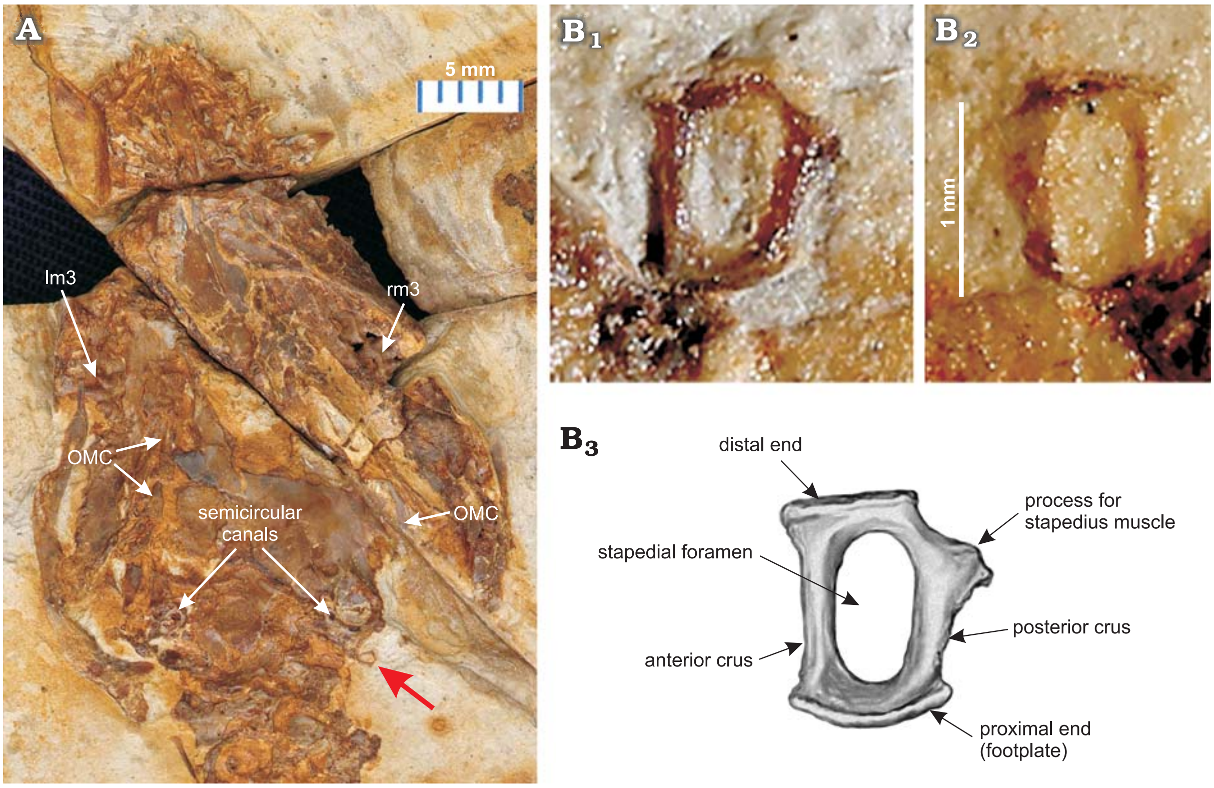

Fig. 1. The skull and right stapes of an Early Cretaceous eutriconodontan *Chaoyangodens lii* Hou *et* Meng, 2014 (JZT005-2010) from Liaoning, China (Hou and Meng 2014). **A**. Dorsal view of the skull with the red arrow pointing to the stapes. **B**. Right stapes (B_1, preserved in slab; B_2, mostly impression); B_3, drawing in dorsal view. Abbreviations: lm3, left m3; OMC, ossified Meckel's cartilage; rm3, right m3.

The ear region on each side of the skull is in poor preservation, but can be identified by exposed cross sections of the semicircular canals. More detailed description of the holotype specimen was presented in Hou and Meng (2014). The morphology and profile of the stapes are well exposed. It is bicrurate and has a large oval stapedial foramen, sufficient for a functional stapedial artery, but it cannot be known whether the artery was present in life. Due to the crushed nature of the specimen there is no cranial structure available for identification of the artery. The stapes measures 1 mm in length, with a maximum width (including the process for insertion of the stapedius muscle) of 0.9 mm. The distal end (in articulation with the incus) and proximal end (the footplate) have the same width, 0.63 mm. This is interpreted as the rostrocaudal length of the stapedial footplate, which approximates the maximum diameter of the footplate. The stapes length as a percentage of skull length is 2.97%, and the skull length to the stapedial footplate diameter ratio is 53.5.

The two crura are nearly parallel and equidistant from the footplate margin, which gives the stapes a rectangular shape in dorsal (lateral) view (Fig. 1B). We interpret the distinctive process on one of the crura as the process for insertion of the stapedius muscle (PISM). In extant mammals the PISM, where present, is on the posterior crus and closer to the stapedial head (Fig. 2C–E); thus, the crus bearing the PISM in *Chaoyangodens* should be the posterior crus and the end of the stapes closer to the PISM is the distal (lateral) end of the stapes (Fig. 1). For those taxa in which the stapedius muscle inserts directly to the stapes head, the process is absent (Doran 1878; Segall 1970; Fleischer 1973; Henson 1974; Novacek and Wyss 1986). The PISM of *Chaoyangodens* is prominent compared to those of extant mammals (Fig. 2), suggesting that the stapedius muscle was relatively large. The homology of this process will be discussed below.

The anterior crus is straight and slightly thinner than the posterior one, as in other mammals (Fig. 2); its cross section is circular judging from the exposed rounded surface of the crus. The posterior crus is slightly curved and arcs posteriorly. The ends of the stapes are almost equal in its width, with the distal end slightly flaring out. The proximal view of the footplate is not available owing to the condition of the specimen preservation. From the exposed edge, the footplate has a slightly convex outline, in contrast to the straight distal end. On slab A the original edge of the footplate slightly projects out from the rest of the stapes. Judging from the exposed portion of the bone, the footplate is most likely an elongate oval with its long axis passing the crura.

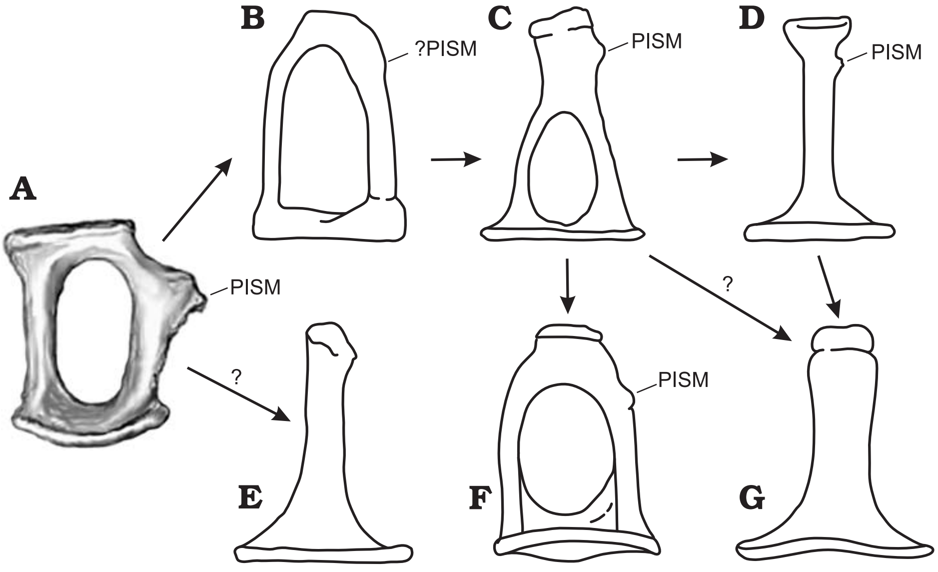

Fig. 2. Comparison and hypothetic transformations of mammalian stapes. **A**. The stapes of *Chaoyangodens lii*, which represents the stapes condition in the TMME and is probably ancestral to those of extant mammals. **B**. The stapes of a Late Cretaceous "unguiculate" eutherian (Archibald 1979). **C**. *Philander* (= *Metachirops*). **D**. *Notoryctes*. **E**. *Orycteropus*. **F**. *Manis*. **G**. *Ornithorhynchus*. B is from Archibald (1979) and C–G from Novacek and Wyss (1986; also see Doran 1878; Segall 1970; Fleischer 1973).

CHARACTER ANALYSES

Shape of the stapes. — The skull of *Chaoyangodens* preserves the ossified Meckel's cartilage, which indicates presence of the TMME, in which the incus fully functioned for hearing. The shape of the stapes must reflect its articulation with the incus. The broad distal end of the stapes indicates that the incudostapedial articulation is sizable and that the incus probably did not have a slender long process and a restricted lenticular process (Doran 1878; Segall 1970; Fleischer 1973; Henson 1974; Novacek and Wyss 1986). This is evidenced by the morphology of the incus in the eutriconodontan *Liaoconodon* (Meng *et al.* 2011). As Meng *et al.* (2011) pointed out, the incus of *Liaoconodon* is proportionally larger than those of extant mammals and its long process is actually shorter than its short process, suggesting that the long process homologous with those of extant therian mammals was not fully developed in *Liaoconodon.*

For early mammaliaforms there are two hypotheses for the stapes-quadrate (incus) articulation: The stapes has a broad end-on-end contact with the quadrate; or it has a restricted contact with the quadrate and simultaneously maintains contact with the tympanic membrane by an extrastapes, as discussed in many studies (*e.g.*, Westoll 1943, 1944; Hopson 1966; Allin 1975, 1986; Parrington 1949, 1979). The former hypothesis appears to be favored because in all therapsid groups the stapes is considerably reduced in size and retains an end-on contact with the quadrate (Allin 1975; Allin and Hopson 1992). The end-on broad contact between the quadrate and the stapes is usually reflected by a broad distal end of the stapes, as in *Brasilitherium*, *Thrinaxodon*, *Exaeretodon*, *Probainognathus*, *Pachygenelus*, and *Haldanodon* (Watson 1953; Estes 1961; Bonaparte 1966; Allin 1975; Parrington 1979; Kermack *et al.* 1981; Novacek and Wyss 1986; Lillegraven and Krusat 1991; Allin and Hopson 1992; Crompton and Luo 1993; Crompton 1995; Rodrigues *et al.* 2013; Ruf *et al.* 2013).

In *Morganucodon* only the proximal part (footplate) of the stapes is known, but a broad distal end of the stapes is reconstructed to articulate with the stapedial process of the quadrate and to prevent the medial displacement of the latter (Kermack *et al.* 1981). A partial stapes of *Sinoconodon* was figured in Crompton and Luo (1993, figs 4.11–4.12), in which it seems that only the anterior crus and partial distal end of the stapes are preserved and visible. From what can be seen, the stapes of *Sinoconodon* probably has a broad distal end.

The stapes of *Chaoyangodens* does not readily fit any of the stapes shapes categories recognized by Novacek and Wyss (1986). The parallel crura and rectangular or columellar outline is somewhat comparable to the columelliform-perforate ("rod-like") stapes that is generally distributed among non-mammalian cynodonts, such as *Probainognathus*, *Pachygenelus*, and *Brasilitherium* (Novacek and Wyss 1986; Allin 1973; Allin and Hopson 1992; Luo and Crompton 1994; Crompton, 1995; Rodrigues *et al.* 2013). The columelliform-perforate stapes is proportionally large and relatively massive in those non-mammaliaforms. In this regard, the delicate and small stapes with slender crura of *Chaoyangodens* is more similar to the bicrurate stapes of mammals (Novacek and Wyss 1986). However, the stapes of *Chaoyangodens* differs from the bicrurate stapes in having a broad distal end and roughly parallel crura that give the stapes a rectangular outline in dorsal (lateral) view. Most distinctively, it has a prominent PISM.

Although the stapes of *Chaoyangodens* has a broad distal end, it does not show any sign of an extrastapes, similar to those of non-mammalian cynodonts as illustrated by Allin (1975, pls 4, 5) and Allin and Hopson (1992, p. 594, fig. 28-5; p. 595, fig. 28-6). Compared to other mammals, the stapes of *Chaoyangodens* is most similar to that of the Late Cretaceous “unguiculate” eutherian (Archibald 1979) in having a large stapedial foramen, nearly parallel proximal portions of the crura, and an elongate oval (narrow) footplate. The “unguiculate” eutherian stapes differs from that of *Chaoyangodens* in being proportionally long in relation to its width and in having its distal end narrowed to form the head. Whether the “unguiculate” eutherian stapes has the process for insertion of the stapedius muscle is uncertain (Archibald 1979). Judging from the thickened posterodistal region of the stapes, it is possible that the process was present; if so, it would have been small and near the head of the stapes.

There are numerous variations in the stapes morphology of extant mammals (Doran 1878; Segall 1970; Fleischer 1973; Henson 1974; Novacek and Wyss 1986), but the distal end of the stapes is almost invariably restricted to form the restricted head, and is significantly narrower than the proximal end or the footplate (Meng 1992). This condition is also applicable to multituberculates where the stapes is known: it can be either columelliform as in the Tertiary *Lambdopsalis* (Meng 1992) or stirrup-shaped as interpreted in the Late Cretaceous *Kryptobaatar* (Rougier *et al.* 1996a). A narrow stapedial head conforms to the shape of the incus. In therian mammals, the incus usually has a slender, long stapedial process (*crus longum*) that ends as a restricted lenticular process; the latter often bends at a right angle to the long process and articulates to the narrow head of the stapes (Doran 1878; Segall 1970; Fleischer 1973; Henson 1974; Novacek 1993).

Size of the stapes. — In understanding the trend of stapes reduction during mammalian evolution, the relative size of a stapes is usually judged by comparing the footplate diameter and stapes length to the length of the skull. The ratio of skull length to the footplate diameter is useful in that the latter can be estimated from the size of the fenestra vestibuli in specimens that do not have the stapes preserved, although the dimensions of the footplate are slightly smaller than those of the fenestra vestibuli because the annular stapedial ligament connecting the footplate to the fenestra vestibuli is not preserved in fossils. However, it should be cautioned that, in non-mammalian synapsids, the rim of the large footplate overlaps the rim of the smaller fenestra vestibuli (Allin and Hopson 1992; see below).

The footplate length is about 90% of that of the fenestra vestibuli in *Haldanodon* (Lillegraven and Krusat 1991) and *Brasilitherium* (Rodrigues *et al.* 2013). Where it is known, the stapes is usually robust in non-mammalian cynodonts (Watson 1953; Estes 1961; Estes 1961; Bonaparte 1966; Allin 1975; Parrington 1979; Kermack *et al.* 1981; Novacek and Wyss 1986; Rowe 1988; Lillegraven and Krusat 1991; Wible 1991; Allin and Hopson 1992; Wible and Hopson 1993; Crompton and Luo 1993; Rodrigues *et al.* 2013; Ruf *et al.* 2013). In *Morganucodon* the skull length (26 mm) to the footplate diameter (0.6 mm) ratio is about 43, contrasting with a value of 110 in an adult *Tachyglossus* (Kermack *et al.* 1981), so that these authors considered the size of the stapes in *Morganucodon* to be enormous in comparison with that of monotremes, and thus concluded that the stapes of *Morganucodon* is more comparable with that of non-mammalian therapsids than with modern mammals. In *Haldanodon* the skull length (35 mm) to the footplate diameter (0.993) ratio is about 35.2. This ratio was regarded as the largest known among terrestrial mammals, a primitive feature that *Haldanodon* shares with its cynodont ancestors (Lillegraven and Krusat 1991). A new specimen of the stapes of *Haldanodon* (MGL 6722) has a maximum footplate length of 0.85 mm and the estimated skull length of MGL 6721 (Ruf *et al.* 2013, fig. 1A) is 37 mm, which together yield a ratio of 43.5, similar to that of *Morganucodon.* Based on the measurements from some cynodonts (Parrington 1949), the ratio of the skull length to the maximum width of the footplate (the proximal end) of the stapes is 21.4 for *Thrinaxodon*, 17 for *Galesaurus*, and 24.8 for *Trirachodon.* The same ratio is 22.6 for *Brasilitherium* (Rodrigues *et al.* 2013).

The skull length to the maximum footplate length ratio is 53.5 in *Chaoyangodens*, indicating that the stapedial footplate is significantly smaller than that of non-mammalian cynodonts but larger than those of extant mammals, such as *Tachyglossus*. This ratio suggests a general trend of the stapedial footplate reduction toward the mammalian condition. However, in mammals with a highly specialized auditory system, such as the multituberculate *Lambdopsalis* (Miao 1988; Meng and Wyss 1995), the stapedial footplate can be proportionally large. The skull length to footplate diameter is less than 35 in *Lambdopsalis* (Meng 1992).

The stapes length to skull length ratio is another parameter of stapes size and has been used as a quantitative character in phylogenetic reconstruction of mammals (Wible 1991). Complete stapes are seldom preserved in early mammaliaforms, such as *Morganucodon* (Kermack *et al.* 1981) and *Haldanodon* (Lillegraven and Krusat 1991; Ruf *et al.* 2013), so that the actual length of the stapes is unknown in these forms. However, the stapes length can be approximated from the distance between the fenestra vestibuli and the quadrate articulation in skulls where relevant elements are in anatomical positions (Wible 1991). Wible (1991; also Wible and Hopson 1993) thus recognized a large stapes as the primitive condition, with stapes length as a percentage of skull length from 7.5 to 13% in non-mammaliaform taxa. Based on actual measurements of the stapes (Parrington 1949), the ratio of stapes length to skull length is 8% for *Thrinaxodon*, 9.4% for *Galesaurus*, and 12.1% for *Trirachodon*. The same ratio is 9% for *Brasilitherium* (Rodrigues *et al.* 2013). The derived condition is a small stapes, with the percentage ranging from 3 to 5.5% in extinct mammaliaform taxa such as *Sinoconodon*, morganucodontids, multituberculates, and *Vincelestes*; and 0.05 to 4.2% in extant mammals (Wible 1991). The percentage ranges of extinct mammaliaforms and extant mammals partly overlap. The actual measurement of the stapes length of the multituberculate *Lambdopsalis* is 2.3 mm (Meng 1992), about 3.3% of an adult skull length, which falls into the overlapping range of the two categories. As a member of the extinct eutriconodontans, the stapes/skull length ratio is 2.97% for *Chaoyangodens*, smaller than those of extinct basal mammaliaforms. It is clear that the relative size of the stapes of *Chaoyangodens*, either the footplate diameter or the stapes length, is well in the range typical for extant mammals. The small stapes of *Chaoyangodens* is consistent with the size reduction of other ear ossicles, as revealed in the eutriconodontan *Liaoconodon* (Meng *et al.* 2011).

Stapedial foramen. — A columelliform-imperforate stapes, like that of monotremes, was once considered as representing the primitive mammalian condition (Doran 1878; Gregory 1910; Segall 1970). More works, however, favor the stapes perforated by the stapedial foramen to be primitive for mammals (Goodrich 1915, 1930; Kuhn 1971; Henson 1974; Fleischer 1978; Novacek and Wyss 1986; Novacek 1993; Lillegraven and Krusat 1991; Wible 1991; Meng 1992; Wible and Hopson 1993; Gaudin *et al.* 1996; Rougier *et al.* 1996a), for the reason that a perforate stapes is present in many non-mammalian cynodonts close to crown mammals, such as *Thrinaxodon, Exaeretodon, Probainognathus*, *Pachygenelus*, *Brasilitherium*, *Sinoconodon*, *Morganucodon*, and *Haldanodon* (Watson 1953; Estes 1961; Bonaparte 1966; Allin 1975; Parrington 1979; Kermack *et al.* 1981; Novacek and Wyss 1986; Rowe 1988; Lillegraven and Krusat 1991; Wible 1991; Allin and Hopson 1992; Wible and Hopson 1993; Crompton and Luo 1993; Rodrigues *et al.* 2013; Ruf *et al.* 2013). Probably because of its relatively robust construction in non-mammalian cynodonts, the stapes in these forms is better preserved compared to the typical mammalian stapes. Novacek and Wyss (1986) also argued that developmental studies of extant mammals show persistence of the stapedial foramen and reduction or loss of the foramen to form the imperforate stapes, as in *Perameles* sp. and *Dasyurus viverrinus* (see Sánchez-Villagra *et al.* 2002), but there is no case in which the perforate condition is plausibly derived from an imperforate condition. The stapes of *Chaoyangodens* lends additional support to the notion that a perforate stapes is primitive for mammals.

Presence of a sizable stapedial foramen is suggestive, but not conclusive, for presence of the stapedial artery. Because the ear region of JZT005-2010 is poorly preserved, there is no other evidence for the existence of the artery. However, the stapedial artery as a common feature is present during development in almost all extant mammals, although it is lost by the adult stage in all marsupials and in some placentals (Wible 1987; Wible *et al.* 2001). An intrastapedial course of the stapedial artery associated with the rod-like stapes has been considered a primitive condition for mammals (Goodrich 1930; Novacek and Wyss 1986). This hypothesis is consistent with the stapes morphology of *Chaoyangodens* (see cautionary note above in “shape of stapes” section).

Given a phylogeny in which Mammalia includes therians, monotremes, eutriconodontans, and multituberculates (Luo *et al.* 2002, 2007; Kielan-Jaworowska *et al.* 2004; Rowe *et al.* 2008); and the mosaic distribution of stapedial morphology within mammals (Doran 1878; Fleischer 1973, 1978; Novacek and Wyss 1986), the columelliform stapes (Fig. 2D) probably evolved by reduction of the stapedial foramen, and did so independently several times within multituberculates, monotremes, marsupials, and placentals.

Stapedial footplate. — In basal mammaliaforms, such as *Morganucodon* (Kermack *et al.* 1981) and *Haldanodon* (Lillegraven and Krusat 1991; Ruf *et al.* 2013), the stapedial footplate is nearly rounded in proximal view. Multituberculates appear to have a similar condition, as evidenced by preserved stapes or the shape of the fenestra vestibuli (Miao and Lillegraven 1986; Wible 1990; Meng 1992; Fox and Meng 1997). In extant mammals, the stapedial footplate is circular in monotremes but varies considerably in therians (Doran 1878; Fleisher 1973; Zeller 1993; Nummela and Sánchez-Villagra 2006). A nearly rounded footplate of the stapes or the fenestra vestibuli has been considered to be a primitive condition in mammals, in contrast to a more elliptical (derived condition) footplate (Segall 1970; Archibald 1979).

The stapedial footplate is probably elongate oval in *Chaoyangodens*. An elongate oval footplate is present in the stapes of various mammals, such as the Cretaceous "unguiculate" eutherian (Archibald 1979), the marsupial *Petaurus breviceps* (Nummela and Sánchez-Villagra 2006), the placental *Tarsius spectrum* (Coleman and Boyer 2011, fig. 6j), and even humans (Quam *et al.* 2014). The footplate shape can be approximated from the fenestra vestibuli for those fossil taxa in which the stapes is not preserved. However, this is only applicable for species in which the stapes fits in the fenestra vestibuli and connects to the rim of the fenestra vestibuli by the annular ligament. Allin and Hopson (1992, p. 596) noted that, in all non-mammalian synapsids, the rim of the large footplate overlaps the rim of the smaller fenestra vestibuli and that this overlapping would have prevented the stapes from being driven into the inner ear. This overlapping relationship means that the size of the footplate is larger than the fenestra vestibuli and that the stapes may not vibrate as an entity in a piston-like manner as in extant mammals; instead, sound pressure waves were propagated along it (Watson 1954). The overlapping footplate-fenestra vestibuli relationship does not seem to be present in *Brasilitherium*, *Haldanodon* (Lillegraven and Krusat 1991; Rodrigues *et al.* 2013; Ruf *et al.* 2013), and *Morganucodon*, as reconstructed by Kermack *et al.* (1981).

Homology of the PISM. — Although the stapes was discovered in the mid sixteenth century (Mudry 2013), its homology still remains controversial. It is known that the three middle ear ossicles are derived from the neural crest and are endochondral bones, of which the stapes originates from the second arch, whereas the malleus (the goniale, which fuses to the malleus, is a dermal bone) and incus are first arch derivatives (Goodrich 1930; De Beer 1937; Crompton and Parker 1978; Kontges and Lumsden 1996; Tucker *et al.* 2004; Chapman 2011; Kitazawa *et al.* 2015). The homology of the stapes can be viewed in two different senses. First, in terms of developmental biology, it remains an open question as to whether the stapes is derived from a unique source of the second branchial (hyoid) arch (Rodríguez-Vázquez 2005, 2009; Rodríguez-Vázquez *et al.* 2006) or is from dual sources, with the footplate originating from the otic capsule and the rest of the stapes representing the dorsalmost derivative of the second branchial arch (Cauldwell and Anson 1942; Anson *et al.* 1960; Masuda *et al.* 1978; Ars 1989; Mallo 1997; Nandapalan and Tos 2000; Whittemore *et al.* 2013). Some authors suggest that development of the stapes is required for formation of the fenestra vestibuli (Rijli *et al.* 1993), whereas others indicate that this ossicle is not essential for formation of the fenestra vestibuli but that the development of the two structures, even if it occurs independently, must be coordinated (Mallo 1997, 2001; Kanzler *et al.* 2000).

Second, from an evolutionary perspective, the views about the homology of the stapes across different vertebrate groups are diverse. Summarizing the work by others (Goodrich 1930; Westoll 1943; Parrington 1979), Novacek and Wyss (1986) pointed out that the hyomandibula in fishes has been broadly homologized with the columella auris in lower tetrapods, and that fine details of structure and function in the hyomandibula of crossopterygians, which seem to be shared by cynodont therapsids and other tetrapods, are identified. These authors consider the homology of these elements at a more general level to be widely accepted. Furthermore, Novacek and Wyss (1986, pp. 41 and 44) thought that "the mammalian stapes is homologous strictly with the 'reptilian' and bird otostapes" and that "the mammalian stapes is homologous with the proximal columella of sauropsids and other tetrapods, but not with the extra-stapedial elements (distal columella) of these forms". On the other hand, Cambas (1983) considered that in mammals, the stapedial footplate and head represent the otic and quadrate processes of the dorsalmost derivatives of the hyoid arch, respectively, and the styloid process (tympanohyal and stylohyal) represents the dorsal and hyoid processes; thus, the columella is the homologue of the stapes and the styloid process. Cambas' work corroborates the hypotheses that the dorsal process of rhipidistians and basal tetrapods may be present in the mammalian styloid process (Goodrich 1930; de Beer 1937) and that the styloid process also includes the homologue of the hyoid process. Presley (1984) also observed that the mammalian blastema shows reasonable homologues of the otic process (stapes), quadrate process (element of Spence), dorsal process (styloid), and hyoid process (stylohyoid) im-

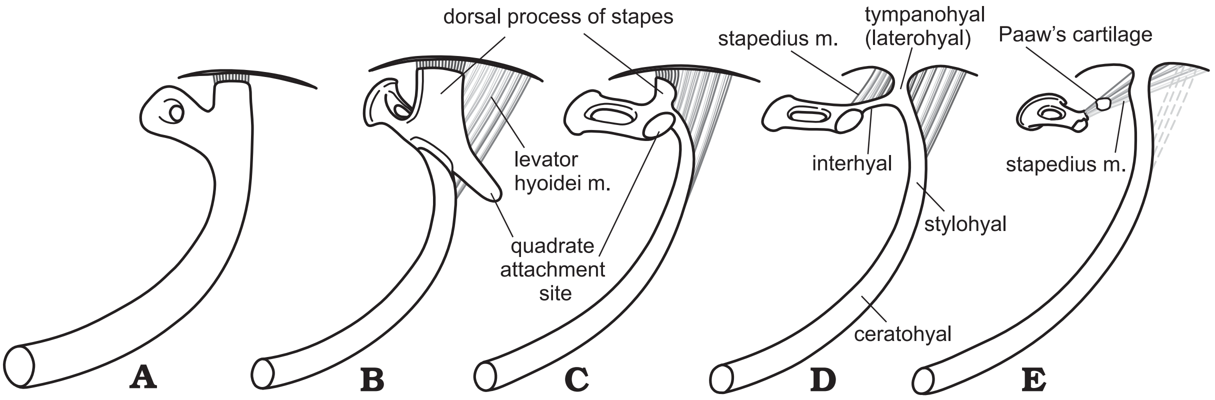

Fig. 3. Diagram showing the development and evolution of the synapsid hyoid arch skeleton, focusing on the stapes and the dorsal process (left side toward anterior aspect). Mesenchymal primordium in a modern mammalian embryo (**A**), compared with adult synapsid conditions (**B**–**E**). **B**. "*Pelycosaur*" condition with a massive stapes having a strong dorsal process attached to the paroccipital process. **C**. Primitive cynodont condition with a lighter stapes having a smaller dorsal process situated posterodistally. **D**. Hypothetical stage based on ontogeny, with fusion of the dorsal process to the paroccipital process, detachment of the dorsal process and hyoid cornu from the stapes except for a slender ligamentous or cartilaginous connection (interhyal). **E**. Modern mammal condition, with a very light stapes having the dorsal process completely detached; and complete differentiation of the stapedius muscle, with the stapedius tendon and its sesamoid cartilage of Paaw. Abbreviation: m, muscle. Modified from Allin and Hopson (1992: fig. 28.3).

plicit in Westoll's (1943, 1945) analysis. Allin (1975, p. 406) explicitly noted that the mammalian stapes "is the homolog of the stapes proper and at least the proximal portion of the extrastapes of reptiles (including the quadrate process)". Allin and Hopson (1992) further recognized that the primitive synapsid stapes appears to include homologs of parts of the sauropsid extrastapes, particularly the quadrate process and the dorsal process; they further hypothesized that both originated from the extrastapes or hyostapes, noting that all except for the quadrate process are lost or detached in extant mammals.

In addition to the aforementioned views on homology of the stapes, the stapes of *Chaoyangodens* raises yet another issue about the homology of the PISM, which in turn is relevant to the development of the stapedius muscle that functions for protecting the inner ear from overstimulation by excessively loud sound and/or for frequency tuning (Wever and Bray 1942; Fleischer 1978). The stapes in early mammals and their close relatives is rare in the fossil record, but where it is preserved, studies have often focused on the general morphology of the stapes, its size, the stapedial foramen, and the footplate (Archibald 1979; Novacek and Wyss 1986; Meng 1992). There is little attention paid to the homology of the PISM, perhaps because the process is such a minuscule structure in extant mammals and is unknown among previously-described Mesozoic mammals, except for its possible presence in the Late Cretaceous "unguiculate" eutherian (Archibald 1979). In contrast, Allin (1975; also in Hopson 1966; Parrington 1979; Allin and Hopson 1992) recognized that an ossified dorsal process is present in at least some members of all therapsid groups; in *Thrinaxodon*, for example, the process extends upward from the posterolateral corner of the stapes toward the paroccipital process. In the Late Triassic mammaliamorph *Brasilitherium riograndensis*, a process near the stapedial head was interpreted as most probably serving as the attachment for the stapedius muscle and was compared to the "strong dorsal process" on the stapes of the *Thrinaxodon liorhinus* (Estes 1961). The stapes of *Brasilitherium* has a larger stapedial foramen and is relatively gracile (Rodrigues *et al.* 2013). The dorsal process or PISM is unknown in *Morganucodon* and *Sinoconodon* because of poor preservation of the stapes in those taxa (Kermack *et al.* 1981; Crompton and Luo 1993).

The question now is whether the PISM is homologous with the dorsal process of the adult therapsid stapes or with another derivative of the second branchial arch. Based on de Beer (1937) and Presley (1984), Allin and Hopson (1992) explained the development and evolution of the synapsid second branchial arch that is relevant to the stapes and related structures (Fig. 3). More detailed and recent developmental studies of the stapes focusing on the human embryo (Rodríguez-Vázquez 2005, 2009; Rodríguez-Vázquez *et al.* 2006) are also illustrative on the homology of the PISM. The general developmental pattern of the stapes is that, during early embryonic stages, the mesenchymal blastema of the second branchial arch in sauropsids and mammals has two processes, the medial and lateral, at its dorsal end. The medial process ossifies in sauropsids as the stapes proper (the otostapes) and in mammals as the entire stapes (Fig. 3). The medial process, called the stapedial anlage in Rodríguez-Vázquez (2005), is a unique combination with two distinct parts: the dorsal part that forms the footplate and the ventral part that is crossed by the stapedial artery during embryonic development and forms the crura and the head of the stapes. The lateral process, which is part of the Reichert's cartilage (Rodríguez-Vázquez, 2005), chondrifies as the dorsal process of the sauropsid extrastapes and fuses to the crista parotica of the otic capsule as the tympanohyal (laterohyal) in mammals (Hanson *et al.* 1962; Cambas 1983; Allin and Hopson 1992; Rodríguez-Vázquez 2005, 2009). In mammals, the homology of the tympanohyal and the dorsal process are supported by their topographic relationships to the jugular vein and hyomandibular branch of the facial nerve, and the articulation with the crista parotica (Cambas 1983; Rodríguez-Vázquez 2005, 2009).

In mammals, a mesenchymal condensation, the interhyal (*interhyale*), temporarily connects the embryonic stapes with the dorsal process (or the cranial end of Reichert's cartilage) in an early stage of development. The interhyal has a thicker proximal part (the stapedial portion), which becomes the tendon of the stapedius muscle and, sometimes, a sesamoid cartilage (of Paaw) within this tendon; whereas the thinner distal (external) part disappears at the beginning of the fetal period. Rodríguez-Vázquez (2005, p. 172) also observed that the stapedius muscle develops independent of the interhyal and joins the interhyal at a later stage of development, so that "the muscle and tendon must therefore have different origins, in contrast to the opinion given by Hanson *et al.* (1962) and Louryan (1993)". Based on the developmental evidence, the PISM of mammalian stapes is most probably homologous with the ossified proximal (stapedial) end of the interhyal on which the tendon of the stapedius muscle attaches, and is not homologous to the dorsal process of the sauropsid extrastapes.

DISCUSSION

In extant mammals and their synapsid kin, the stapes distally articulates with the incus (quadrate). This articulation is conservative and represents the quadrate-hyomandibular joint that was present in ancestral amniotes but was lost in diapsids (Kitazawa *et al.* 2015). The general evolutionary trend for the stapes is its reduction in size from a massive one in non-mammalian cynodonts to a miniscule one to comply with the reduced incus, the malleus, and the ectotympanic bones in mammals. Reduction of the stapes size decreases its mass, and the stapes is in fact the lightest of the ear ossicles (Fleischer 1978). The stapes in extant mammals is characterized by a narrow distal end (the head) so that for stapes with two crura, the crura are not parallel to each other but distally converge in various ways to the head. For those with a narrow columelliform shaft, the head is as wide as, or only slightly wider than, the shaft (Fig. 2D, F, G). This morphology perhaps represents the latest stage of mass reduction of the stapes during the evolution of the mammalian middle ear, which, along with modifications of the incus and malleus, functions for highly sensitive airborne hearing. As recognized by Fleischer (1978), it is much easier to tune a vibrational system, with the stapes being a mass-spring system, to high frequencies if the mass involved is small. Moreover, through the tension of the stapedius muscle, the stapes can be somewhat tilted. Whether this is for protecting the inner ear from overstimulation or for change of frequency response of the ear is unclear, but the articulation between incus and stapes has to allow for some lateral give (Fleischer 1978). A restricted stapedial head seems necessary or at least efficient for such flexibility at the incudostapedial articulation.

The stapes is poorly represented in the Mesozoic fossil record, making it difficult to understand its evolutionary transition within early mammals. Archibald (1979) thought that the perforate stapes is likely the primitive mammalian condition, but he also considered both the columelliform stapes of monotremes and the stirrup-like stapes of the Late Cretaceous "unguiculate" eutherian (Fig. 2) to be derived compared to that of *Didelphis.* The new evidence from *Chaoyangodens*, however, favors an alternative hypothesis that the Late Cretaceous eutherian stapes is probably more primitive than that of *Didelphis* and that the columelliform stapes of monotremes may have evolved independently from that of therians (Fig. 2). Furthermore, the stapes of *Chaoyangodens* lends support to the notion that the rod-like stapes with a broad distal end is a primitive condition for mammals (Novacek and Wyss 1986; Meng 1992; Rougier *et al.* 1996a). From the mandibular middle ear to the TMME the stapes reduces in size, falling in the size range of extant mammals. However, because of the relatively broad distal end, as in *Chaoyangodens*, tension of the stapedius muscle at the TMME stage may work differently from those of the DMME, in that the stapes may not be tilted and the incudostapedial articulation has less flexibility to allow for any lateral give (Fleischer 1978). From the stapes of the TMME to that of DMME of mammals, the most distinct change is the restriction of the distal end of the stapes. Given the diverse phylogenetic hypotheses of mammals (see Meng 2014 and references therein) and the poor fossil record of the stapes in early mammals, it is difficult to map on any phylogeny how the stapes evolved within major clades of mammals. It is highly possible that the stapes with a restricted (narrow) head evolved independently more than once to give rise to a variety of stapes forms in mammalian subgroups (Doran 1878; Fleischer 1973, 1978; Novacek and Wyss 1986).

The interesting issue about the stapes of *Chaoyangodens* is the presence of a distinctive PISM. As noted above, the embryologic evidence of extant mammals shows that the PISM and the dorsal process (tympanohyal) are two different structures, although both are derivatives of the second branchial arch. The PISM is probably homologous with the proximal (stapedial) end of the interhyal instead of the dorsal process of the sauropsid extrastapes. It follows that, if the stapes has the dorsal process, as interpreted in *Thrinaxodon*, the PISM and the tympanohyal would be absent. Similarly, if the tympanohyal is formed at the basicranial region in Mesozoic mammals, as has been interpreted for multituberculates (Wible and Hopson 1995; Rougier *et al.* 1996a; Wible and Rougier 2000) and eutriconodontans (Wible and Hopson 1993, 1995; Rougier *et al.* 1996b; Wang *et al.* 2001; Meng *et al.* 2003), there should be no expression of the dorsal process on the stapes in those forms. For *Brasilitherium riograndensis*, if the process on the stapes is for the attachment of the stapedius muscle, as interpreted by Rodrigues *et al.* (2013), then it should not be the dorsal process, but the PISM. Because the stapes of non-mammaliaform cynodonts lacks the PISM, the development of the PISM and the stapedius muscle would represent innovative structures acquired during the evolution of the mammalian middle ear. Whether the stapedius muscle is for protecting the inner ear from overstimulation or for tuning of sound vibrations, this structure works only with a gracile stapes, probably including taxa such as *Brasilitherium riograndensis*, and is perhaps suggestive for high frequency hearing.

The distinctive PISM of *Chaoyangodens* suggests that the interhyal was less reduced than that of any known adult individuals of extant mammals and that the stapedius muscle was relatively larger than that of extant mammals. Whether similar structures were present in basal mammaliaforms was unclear. However, the stapedius muscle may be inferred from presence of the fossa for the stapedius muscle on the petrosal, which in turn is suggestive of the PISM. The fossa for the stapedius muscle is known in eutriconodontans (Wible and Hopson 1993; Rougier *et al.* 1996b), consistent with presence of the PISM in the eutriconodontan *Chaoyangodens*. The stapedius fossa is not illustrated in the petrosal of *Morganucodon* (Wible and Hopson 1993, 1995), but a deep pit anterior to the paroccipital process and immediately posterior to the rod (the crista interfenestralis) separating the fenestrae cochleae and vestibuli was posited as possibly housing the levator hyoidei muscle; the latter is found in monotremes and is the homologue of the stapedius muscle (Kermack *et al.* 1981). Rougier *et al.* (1996b), following Crompton and Sun (1985), interpreted this feature as an indicator of the stapedius muscle in *Morganucodon*, and noted that a similar depression on the crista interfenestralis occurs in tritylodontids, *Sinoconodon*, *Dinnetherium*, *Megazostrodon*, and *Haldanodon*. The stapedius fossa (stapedial muscle fossa) and the site possibly for the attachment of the tympanohyal were identified in *Haldanodon* (Ruf *et al.* 2013) and *Dryolestes* (Luo *et al.* 2012). In *Brasilitherium riograndensis*, neither the tympanohyal nor the fossa for the stapedius muscle were reported (Rodrigues *et al.* 2013). Absence of the two structures, if confirmed with better material, would favor interpretation of the process on the stapes of *B. riograndensis* as the dorsal process, not the PISM.

In some extant therian mammals, the PISM is small and close to the head (Fig. 2), which probably represents a vestige of the ossified proximal base of the interhyal. In others, the PISM is absent or the stapedius muscle inserts directly to the head so that there is no discernable process on the posterior crus of the stapes (Doran 1878; Segall 1970; Henson 1974; Fleischer 1978; Novacek and Wyss 1986; Novacek 1993). This may be interpreted as reduction or non-ossification of the proximal interhyal in adult therian stapes. However, lack of the PISM in monotremes may require a different interpretation because monotremes do not have the stapedial muscle (Fleischer 1978). Presley (1984) also noted that there is no true stapedius muscle in adult monotremes and that this is probably secondary, owing to the very specialized pattern of the ossicles. Based on the work of Edgeworth (1931, 1935), Wible (1991), and Wible and Hopson (1993) pointed out that the levator hyoidei muscle, from which the stapedius muscle is derived, is present in monotremes, but it takes origin from the ventral edge of the paroccipital process in *Ornithorhynchus* and from the squamosal in *Tachyglossus*. Thus, lack of the stapedius muscle and the PISM on the stapes of monotremes suggest the possibility that the stapes of monotremes does not include the part homologous to the interhyal.

CONCLUSIONS

Of the middle ear ossicles reported from a handful of Mesozoic mammals, the stapes remains the least known. The discovery of the stapes from the Early Cretaceous eutriconodontan *Chaoyangodens* (Hou and Meng 2014) provides the first unambiguous morphology for the structure in eutriconodontans and is the earliest known mammalian stapes. The stapes of *Chaoyangodens* is reduced in size compared to those of non-mammalian cynodonts and is within the size range of extant mammals. Reduction of the stapes is consistent with the reduced incus and malleus as observed in the TMME of the eutriconodontan *Liaoconodon* (Meng *et al.* 2011). The stapes of *Chaoyangodens* has nearly parallel crura and a large stapedial foramen, supporting the notion that the rod-like stapes, penetrated by a large stapedial foramen, is a primitive condition for mammals. The broad distal end of the stapes in *Chaoyangodens* indicates an end-on broad contact with the incus, a primitive retention of the condition seen in basal mammaliaforms. Reduction of the distal end of the stapes to form a narrow head of the stapes in the DMME of extant mammals likewise reduces the mass of the stapes and allows flexibility at the articulation between the stapes and the incus. These modifications of the stapes would contribute to sensitive hearing of high-frequency airborne sounds and are derived features present in extant mammals. The process identified as the PISM on the posterior crus of the stapes remains prominent in *Chaoyangodens*. Based on embryological studies of extant mammals, the distinct PISM of *Chaoyangodens* is hypothesized to be homologous with the ossified proximal end of the interhyal and is probably present in close relatives of mammals that have the stapedius muscle (as reflected by presence of the fossa for the stapedius muscle). The PISM and the stapedius muscle attached to it are probably innovative structures that developed during the evolution of cynodonts toward mammals. Absence of the PISM and lack of the stapedius muscle in monotremes may suggest that the stapes of monotremes does not have the homologue of the PISM. The stapes of *Chaoyangodens* indicates that, during the evolution from the mandibular middle ear to the TMME, the stapes conforms to the change of other ossicles in size and mass reduction. From the TMME to DMME, the stapes reduces its distal end to form a restricted head and the PISM is reduced to a vestige or becomes completely indiscernible.

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ADDENDUM

While this paper was in press, a study by Gaetano and Abdala (2015) appeared, in which the authors presented excellent documentation of the stapes in gomphodont cynodonts and discussed the broader implications for structure of the middle ear among non-mammaliaform cynodonts. Although Gaetano and Abdala's work is largely consistent with some previous observations on the stapes of non-mammaliaform cynodonts, as summarized herein, the authors raised an issue in interpreting the function of the dorsal process present on some stapes they reported. According to Gaetano and Abdala, the dorsal process is a triangular-shaped lamina pointing dorsally or dorsomedially from the dorsolateral portion of the posterior crus in non-mammaliaform cynodonts (except for some specimens of *Thrinaxodon*) and is well-suited for the insertion of a small ligament or muscle, such as Paauw's cartilage or the stapedial muscle. The authors interpreted that the stapedial muscle connected the stapes, by attachment to the dorsal process, to the paroccipital process in basal cynodonts (see Gaetano and Abdala 2015, for detailed discussion and references). This interpretation differs from what we advocate in our paper: we interpret the dorsal process and PISM as different structures based on developmental evidence. If both structures are interpreted as serving for attachment of the stapedial muscle among different groups of cynodonts, then the homology of either the bony process on the stapes or the muscle presumably attached to it, or both, needs to be further investigated within a phylogenetic framework, as well as within embryological context bearing on development of the stapes. Further data and research are needed to address this intriguing homology issue.

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