Editors' choice

The origins of the cochlea and impedance matching hearing in synapsids

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The origin of tympanic hearing in early synapsids is still controversial, because little is known about their inner ear and the function of their sound conducting apparatus. Here I describe the earliest known tympanic ear in the synapsid lineage, the ear of *Pristerodon* (Therapsida, Anomodontia) from the Late Permian of South Africa, which was virtually reconstructed from neutron tomographic data. Although *Pristerodon* is not a direct ancestor of mammals, its inner ear with distinctive cochlear cavity represents a connecting link between the primitive therapsid inner ear and the mammalian inner ear. The anatomy of the sound conducting apparatus of *Pristerodon* and the increased sound pressure transformer ratio points to a sensitivity to airborne sound. Furthermore, the origins of the cochlea and impedance matching hearing in synapsids coincided with the loss of contact between head and substrate, which already took place at least in Late Permian therapsids even before the postdentary bones became detached from the mandible.

Key words: Therapsida, Anomodontia, cochlea, tympanic hearing, Permian, South Africa.

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Introduction

The definitive mammalian middle ear and the extremely elongated mammalian cochlea are unique among vertebrates and enable mammals to hear sound in a wider range of frequencies at an increased frequency resolution (Manley 2010; Luo et al. 2011). However, all tetrapods evolved from aquatic ancestors, which were initially not able to hear airborne-sound, because sound waves in the air are considerably weaker than in water and can only be sensed by animals having an impedance matching middle ear (Tumarkin 1955, 1968; Clack 2002; Manley and Sienknecht 2013; Walsh et al. 2013). Nevertheless, early tetrapods were probably not completely deaf and were able to detect vibrations from the ground by bone conduction via the limbs, the mandible or any other part of the body, because hearing of substrate sound is not much affected with the problem of impedance matching as sound in air (Tumarkin 1955, 1968). Particularly, the mandibular-quadrate-hyomandibular route to the inner ear has been proposed as an important pathway of bone conduction in non-mammalian synapsids (Tumarkin 1955, 1968; Kermack and Mussett 1983; Kermack and Kermack 1984; Allin 1975; Allin and Hopson 1992; Laaß 2014).

It seems reasonable that the ability to hear airborne sound must be of great importance for early tetrapods and evolved sometimes or even several times during the synapsid evolution. However, the search for the origins of tympanic hearing is complicated by the absence of soft-tissue structures in fossils and by the difficulty to infer auditory capabilities from fossil ear structures. Consequently, the origin of tympanic hearing in synapsids is still debated, which is briefly reviewed in the following sections.

Reichert (1837) and Gaupp (1913) already showed that the mammalian middle ear bones, the malleus and incus, are the homologues of the bones of the jaw hinge of primitive amniotes, the articular and quadrate, respectively. Furthermore, the mammalian ectotympanic, which supports the tympanum, is homologous to the angular of primitive amniotes. Therefore, much attention has been paid to the evolutionary origins of the mammalian middle ear in the fossil record, particularly, the detachment of the postdentary bones from the mandible and the position of tympanum and tympanic cavity.

A number of early works focused on the problem of how the mammalian three-ossicle middle ear could have evolved from the reptilian single-ossicle middle ear and the tympanum moved from a postquadrate position to the lower jaw (Goodrich 1930; Westoll 1945; Watson 1953; Parrington

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1949, 1955). As demonstrated by Allin (1975) it is for anatomical and functional reasons very unlikely that the mammalian middle ear evolved from a reptilian-like middle ear by incorporation of the articular (malleus) and the quadrate (incus) between the tympanum and the extracolumella. Instead, he proposed that the mammalian middle ear evolved from the mandibular sound conducting apparatus of therapsids, which was preadapted for hearing by detection of seismic sound from the ground. This is also supported by the interpretation of the "otic notch" in early tetrapods, which was once assumed to be the host for a tympanic membrane, but is now considered as the spiracular notch (Clack 1989, 1993). Consequently, it has been widely accepted that impedance matching middle ears evolved several times independently in different vertebrate groups (Manley 2010; Clack 1997; Müller and Tsuji 2007).

This is consistent with the theory of Allin (1975) according to which the tympanum of the therapsids is not homologous to the reptilian tympanum. It was probably spanned over the mandibular recess at the mandible, which is interpreted as the forerunner of the mammalian tympanic cavity (Allin 1975; Allin and Hopson 1992). Particularly, in basal therapsids much of the mandibular recess was covered by a thin bony plate of the angular, the reflected lamina, which probably also served as a sound receiving element (Allin 1975; Allin and Hopson 1992; Maier and van den Heever 2002). Alternatively, the reflected lamina and the mandibular recess were interpreted as a surface for muscle attachment (Janensch 1952; Hopson and Barghusen 1986; King 1981; Kemp 2007), which is supported by the fact that the reflected lamina in basal and large therapsids is often relatively thick and, thus, seems inefficient as sound receiver.

Allin's (1975) interpretation has been widely accepted, because it explains the origin of the mammalian middle ear only by a miniaturisation of the mandibular apparatus that already had some auditory function in the premammalian therapsids, and the evolutionary addition of a new secondary jaw articulation to release mandibular ear bones from the strain of the masticatory muscle force (Crompton 1972; Allin 1975; Crompton and Hylander 1986; Maier and van den Heever 2002; Luo 2011). Interestingly and as an exception to the overall trend of evolution of synapsids, anomodonts show an opposite evolutionary trend to increase the mass of the postdentary bones (Sidor 2003).

Allin's (1975) theory seems to be also supported by the transformation of the stapes and modifications in skull architecture in early tetrapod evolution. Accordingly, the stapes, which was just a massive strut to support the braincase in pelycosaurs, more and more lost its structural function and became a more slender and horizontally orientated bone in therapsids, which was able to vibrate in the fenestra vestibuli (Lombard and Bolt 1979; Allin and Hopson 1992; Clack 2002). At the same time the occipital and palatal region consolidated and came into firmer contact with the braincase (Clack 2002). Furthermore, the anatomy of the quadrate in advanced non-mammalian synapsids, which formed together with the articular the primary jaw articulation as in modern reptiles, suggests restricted mobility and a dual function for hearing and feeding (Allin and Hopson 1992; Luo and Crompton 1994). The same seems to be true for the postdentary bones in advanced therapsids, which were not firmly fused with the rest of the mandible (Kemp 2007) and possibly able to vibrate slightly.

There is wide agreement that this sound conducting apparatus of therapsids was, if at all, restricted to low-frequency hearing due to its low compliance and the high masses and inertia of its elements, which was necessary to withstand the forces from feeding (Allin 1975; Allin and Hopson 1992; Maier and van den Heever 2002; Kemp 2007). But, the question, when the mandibular ear of therapsids became sensitive to airborne sound is highly controversial, because soft-tissue structures are not preserved and the acoustic properties of the sound conducting apparatus cannot be exactly determined in fossil taxa. These uncertainties are also reflected in the results of previous studies regarding the hearing capabilities of early synapsids, which considerably differ from each other. For example, a study about hearing in the mammaliaform *Morganucodon*, which possessed a cynodont-like middle ear, revealed sensitivity to low-frequency airborne sound up to about 1 KHz (Kermack et al. 1981). According to another study *Morganucodon* was able to hear airborne sound up to 10 KHz, which is comparable to modern mammals (Rosowski and Graybeal 1991; Rosowski 1992). In contrast, Kemp (2007), who investigated the acoustic function of the ear of the cynodont *Chiniquodon*, came to the conclusion that the non-mammalian cynodont ear was inefficient to hear airborne sound due to the dual function of the postdentary bones for feeding and hearing and their high mass and low compliance. He assumed that the fully mammalian acoustic transformer system, with tympanic cavity and tympanic membrane, could only have evolved after the origin of the dentary-squamosal jaw articulation (Kemp 2007).

A further indication for the hearing range is the length of the cochlea, which is used in reptiles and birds as a proxy to deduce hearing capabilities of extinct species (Walsh et al. 2009). The hearing range of mammals also roughly correlates with cochlear length among species within clades, but may also be influenced by basilar membrane width (Manley 1973, 2012). The existence of a basilar papilla in non-mammalian synapsids seems very likely, because a small basilar papilla is already present in the coelacanth *Latimeria* (Fritzsch 1987) which is considered to be homologous to the basilar papillae of all vertebrates (Manley 2012). Unfortunately, in most therapsids the length of the basilar membrane cannot be inferred from the shape of the bony labyrinth, because the inner ears of therapsids lack distinctive cochlear cavities. Such "primitive" inner ears with undifferentiated, straight, elongated tubular vestibules and fenestrae vestibuli situated at the ventral apex of the vestibule are described for pelycosaurs, most anomodonts and gorgonopsians (e.g., Broom 1912; Sollas and Sollas 1914; Cox 1962; Olson 1944; Fourie 1993; Sigogneau 1974). The same is true for the inflated vestibule of the

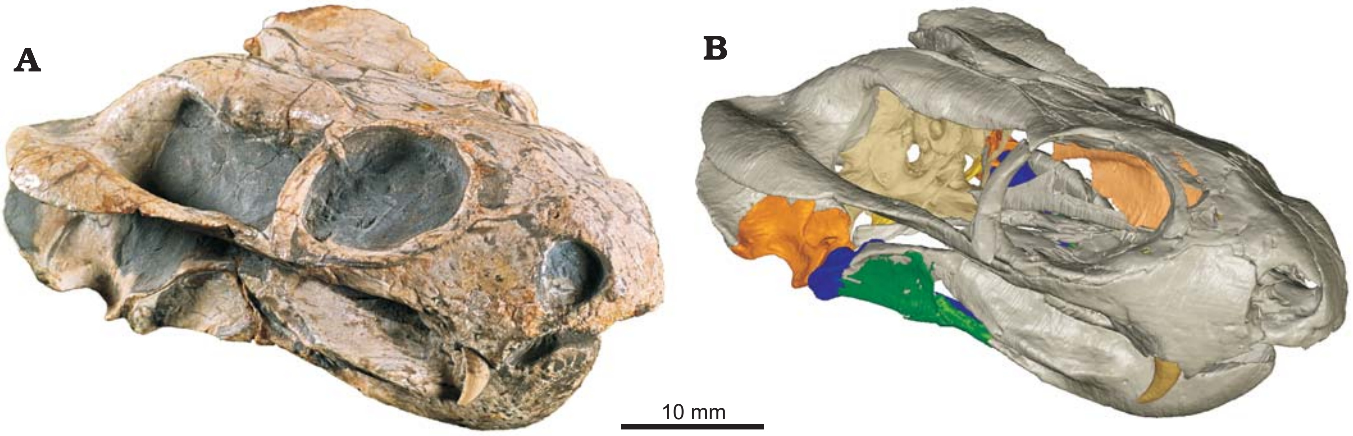

Fig. 1. The skull of the non-mammalian synapsid *Pristerodon mackayi* Huxley, 1868 (MB.R.985) from the Late Permian of Biesjespoort, South Africa. Photograph (**A**) and virtual 3D model (**B**) of dorsolateral view.

Permian anomodont *Kawingasaurus fossilis*, which is interpreted as having adaptation to seismic sound detection (Laaß 2014) as in the Cretaceous multituberculates *Catopsalis* and *Meniscoessus* (Luo and Ketten 1991), the Paleocene multituberculate *Lambdopsalis bulla* (Miao 1988) and possibly also other multituberculates (Laaß 2014: fig. 8). Until now distinctive cochlear cavities are only known for the anomodont *Niassodon mfumukasi* (Castanhinha et al. 2013) and some advanced cynodonts such as *Thrinaxodon* (Estes 1961; Fourie 1974; Rowe et al. 1995), *Massetognathus* (Quiroga 1979), *Probelesodon* (Quiroga 1979), *Probainognathus* (Luo et al. 1995), *Yunnacodon* (Luo 2001) and *Brasilitherium riograndensis* (Rodrigues et al. 2013). The straight or slightly curved cochlear cavities of Mammaliaformes are only slightly longer (Luo et al. 1995; Kielan-Jaworowska et al. 2004). Generally, all cochlear cavities of non-mammalian synapsids are very short, i.e., they had lengths up to 2 mm, which is consistent with the hypothesis of a small hearing range in non-mammalian synapsids. Nevertheless, the presence of small cochlear cavities in non-mammalian synapsids shows that the cochlea is much older than the mammalian middle ear and its evolution already began before the postdentary bones became detached from the mandible and the dentary-squamosal jaw articulation evolved. In contrast to the transition of the middle ear from cynodonts to mammals, little attention has been given to the origin and early evolution of the cochlear cavity in therapsids which is, therefore, the subject of this paper.

Institutional abbreviations.—MB.R, Museum of Natural History in Berlin, Germany; SAM-PK, South African Museum, Cape Town, Republic of South Africa.

Material and methods

Material.—The subject of this study was the holotype of the uncertain taxon *Cryptocynodon schroederi* from the collection of the Museum of Natural History in Berlin (number MB.R. 985; Fig. 1), which was named by Janensch (1952). The specimen comes from Biesjespoort, Farm Modderfontein (Cape Province), South Africa, and according to Janensch (1952) it derives from the former *Endothiodon* Zone, which corresponds to the *Tropidostoma* Assemblage Zone sensu Rubidge (1995). According to King and Rubidge (1993) the specimen is slightly younger and it is more likely that it comes from the *Aulacephalodon–Cistecephalus* Zone, which corresponds to the *Cistecephalus* Assemblage Zone sensu Rubidge (1995). The results of this study support the assumption that *Cryptocynodon schroederi* is a junior synonym of *Pristerodon mackayi* (see SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Laass_SOM.pdf).

Except a slight dorsoventral distortion the skull is virtually complete and extraordinarily well preserved. Almost all sutures of the cranial bones are visible, because of the good contrast between the light grey colored skull bones and the dark grey matrix.

Additional material of *Pristerodon mackayi* Huxley, 1868 (SAM-PK-K1658; SAM-PK-10153; see SOM 1: figs. S1, S2), which is housed in the collection of the South African Museum, Cape Town, was used only for comparison and for reconstruction of the shape of the reflected lamina. Detailed investigations of the specimens including measurements of the thickness of the reflected laminae were not possible, but are planned in a future study.

Neutron tomography and reconstruction of the tomographic volume.—This work is based on an experiment performed at the Swiss spallation neutron source SINQ, Paul Scherrer Institute, Villigen, Switzerland. The specimen was scanned at the beamline ICON using cold neutron radiation.

Similar to Computed Tomography neutron radiographic images were taken from different perspectives over a range of 360°. In this experiment 1125 projections of the fossil skull in steps of 0.32° were produced. The exposure time was ca. 60 seconds per projection. For the transformation of neutron radiation into visible light a 50 µm LIF detector

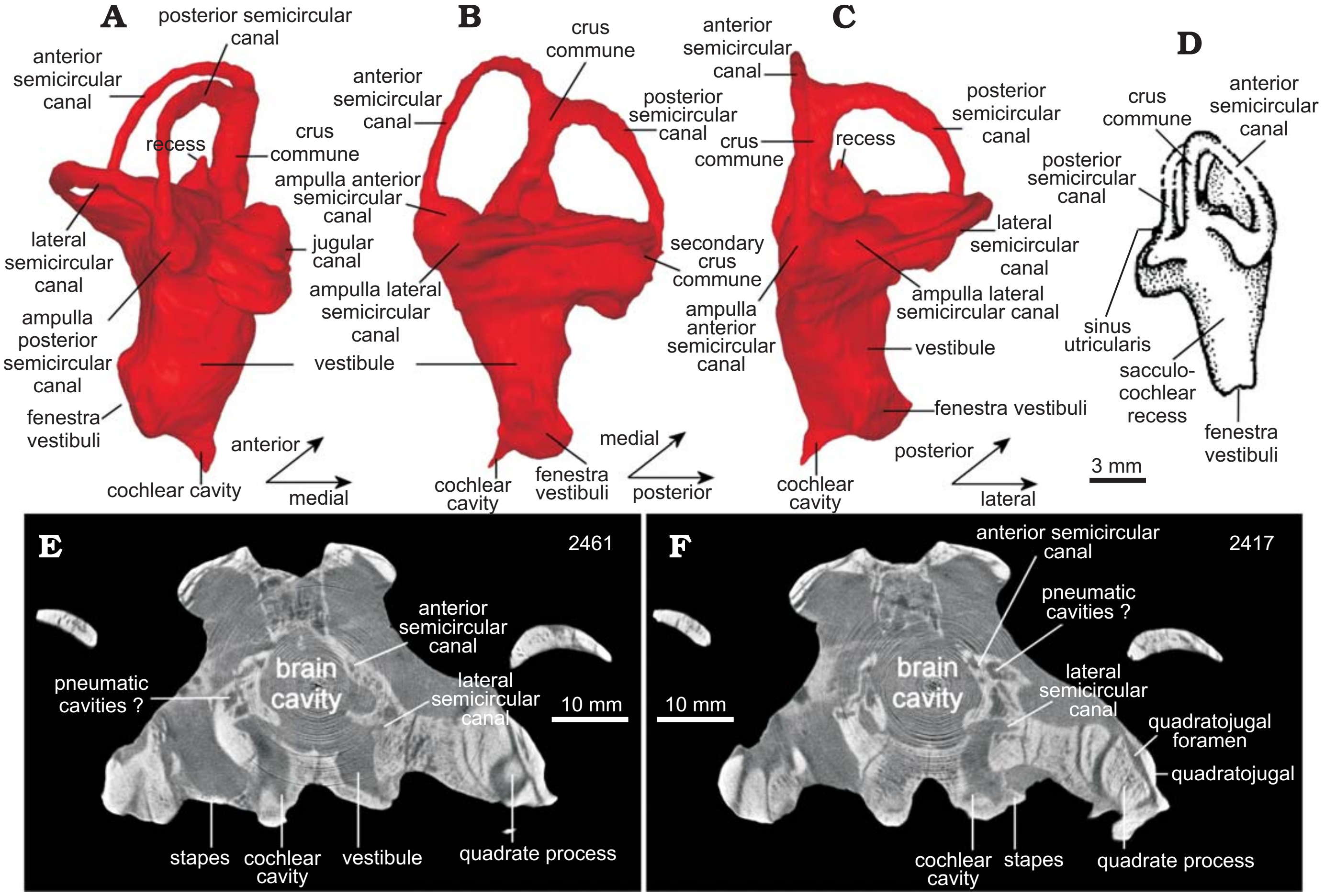

Fig. 2. The inner ear labyrinth of the non-mammalian synapsid *Pristerodon mackayi* Huxley, 1868 (MB.R.985) from the Late Permian of Biesjespoort, South Africa. Virtual cast of the left inner ear labyrinth in posterior (**A**), lateral (**B**), and anterior (**C**) views. Otic region including cochlear cavity of the left (**E**, tomographic slice 2461) and right (**F**, tomographic slice 2417) inner ear. **D**. Inner ear reconstruction of *Pristerodon* by Barry (1967).

was used. After each projection the shadow image produced by the CCD system was projected by the lens system from the detector to the CCD camera. The camera used for this experiment was a PCO pco. 4000 camera, SN: 8000001017 combined with a Zeiss, Makro-Planar 2/100 ZF.2 T*, SN: 15823223 lens. The tomographic volume was reconstructed by using the software Octopus 8.5 (Inside Matters; http://www.octopusreconstruction.com/en/home). The tomographic slices of MB.R.985 have a spatial resolution of 28.6 µm per pixel.

3D modeling and visualisation of the skull of *Pristerodon*.—3D modelling and visualisation of the tomographic slices was done with the software AMIRA 5.4 (FEI Visualization Sciences Group; http://www.vsg3d.com/). Structures of interest such as the bones of the skull, the endocasts of the inner ears and several canals of nerves and blood vessels were vectorized slice by slice with the segmentation tool of AMIRA. After smoothening and polygon reduction the regions of interest were saved as Wavefront files (OBJ). After this, the Wavefront files were reassembled, colored and integrated into 3D PDF files with the software Simlab Composer 2014 SP1 (Simlab Soft; http://www.simlab-soft.com/).

Measurements.—Volumes of bones or cavities as well as lengths of internal structures of interest were determined in the 3D model of *Pristerodon* using the volume determination tool and the 3D measurement tool of AMIRA 5.4, respectively. The dimensions of the inner ear were measured in the 3D model following Spoor and Zonneveld (1995) and Schmelzle et al. (2007). The extent of the reflected lamina, which is incomplete in MB.R.985, was reconstructed using the specimens of *Pristerodon* SAM-PK-K1658 and SAM-PK-10153.

Results

The subject of this study is the ear region of *Pristerodon mackayi* (MB.R.985) from the Late Permian of South Africa (Fig. 1), which is described in detail in the following sections. As the internal cranial anatomy of *Pristerodon buffaloensis*, which is also considered to be a junior synonym of *Pristerodon mackayi* (Keyser 1993), has already been described by Barry (1967), the following description only focuses on new observations revealed from neutron tomography and on features being crucial for functional interpretation. All measurements are summarized in SOM 1: table S1.

Description of the osseous labyrinth.—Remarkably, the osseous labyrinth of *Pristerodon* (MB.R. 985; Fig. 2A–C, E, F) differs from the specimen described by Barry (1967) (see Fig. 2D), who reconstructed a straight and tubular inner ear vestibule without distinctive cochlear cavity and a fenestra vestibuli at the ventral apex of the vestibule. Neutron tomography showed that the vestibule of *Pristerodon* (MB.R.985) is curved, i.e., its dorsal portion is dorsoventrally oriented and its ventral part slopes laterally. Similar vestibules occur in the anomodont *Niassodon mfumukasi* (Castanhinha et al. 2013) and in the "Therocephalian B" (Olson 1944). The vestibule volume of MB.R.985 is 75.14 mm^3, which is in relation to the skull length considerably smaller than those of the anomodont *Kawingasaurus fossilis* (Laaß 2014). Due to the curved vestibule the fenestra vestibuli has a lateral position. Dorsally, small recesses are present on both inner ears. Ventrally, a small cochlear cavity is developed. It is slightly anteriorly-oriented and has a length of about 3 mm. Among anomodonts a distinctive cochlear cavity has only been reported for *Niassodon mfumukasi* (Castanhinha et al. 2013).

The subcircular semicircular canals resemble the condition in mammals. The largest is the anterior canal, the smallest is the lateral semicircular canal. Medially, both anterior and posterior semicircular canals derive from the crus commune, which is about 4 mm long. Caudally, between the descending posterior semicircular canal and the vestibule a secondary crus commune is developed. The angles between the anterior and the posterior semicircular canal as well as the angle between the anterior and the lateral semicircular canal are both 78°. The angle between the posterior and the lateral semicircular canal is slightly larger (82°).

Finally, it should be mentioned that the osseous labyrinth is encircled by numerous cavities, which are irregulary shaped and connected to each other by foramina and canals (Figs. 2D, E, 3). As revealed from the neutron tomographic images the cavities are bordered by smooth walls as it is known for tympanic sinuses and, thus, differ in this feature from resorption cavities in cancellous bone. Whether or not this system of cavities is connected via pneumatic foramina to the space around the stapes is uncertain.

Description of the stapes.—Both stapes are still in natural position, but not suturally attached with the quadrate as it has been claimed for *Pristerodon buffaloensis* (Barry 1967). The stapes is collumelliform and lacks a stapedial foramen (Fig. 4). It has a length of about 11 mm and is horizontally orientated. Similar as in *Niassodon mfumakasi* (Castanhinha et al. 2013) the stapes of *Pristerodon* is medially narrower and tapers laterally, where the stapedial head forms a dorsoventrally flattened spatulate facet which contacts the quadrate-quadratojugal complex. The stapedial head has a dorsoventral length of 5.35 mm and an anteroposterior width of 2.59 mm. The footplate has an oval shape with a maximum diameter of 4.33 mm and a minimum diameter of 3.53 mm, which amounts to an area of about 12 mm^2. There is no sign for a stapedial process of the stapes.

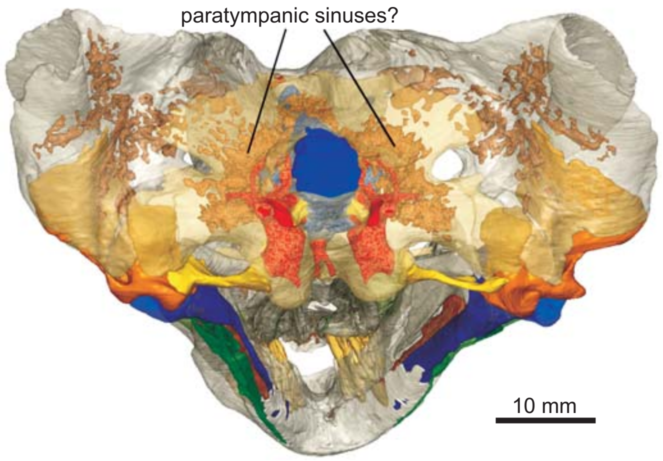

Fig. 3. Distribution of cavities in the otic region of the non-mammalian synapsid *Pristerodon mackayi* Huxley, 1868 (MB.R.985) from the Late Permian of Biesjespoort, South Africa. Note the concentration of a number of large cavities (brown) around the inner ears, which are connected to each other. The neurocranium is shown transparent.

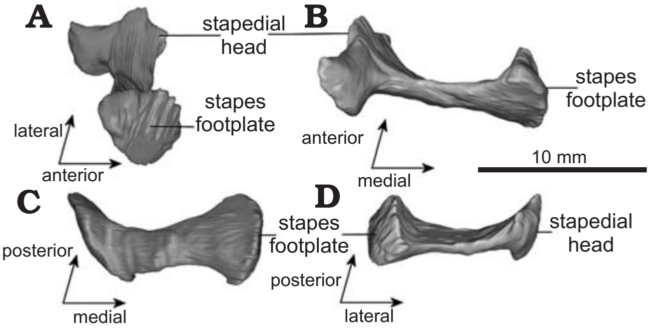

Fig. 4. Virtual reconstruction of the left stapes of the non-mammalian synapsid *Pristerodon mackayi* Huxley, 1868 (MB.R.985) from the Late Permian of Biesjespoort, South Africa; in medial (**A**), posterior (**B**), ventral (**C**), and anterior (**D**) views.

Description of the quadrate-quadratojugal complex.—As quadrate and quadratojugal are indistinguishably fused at the base of the quadratojugal, it is described here as a single unit (Fig. 5). Important for the functional interpretation is that the quadrate process and the quadratojugal are not abutted or dorsally fused as it has been claimed for other anomodonts (Luo and Crompton 1994). Instead, they are clearly separated from each other by a narrow, deep cleft, the "quadratojugal foramen" as in the anomodont *Kawingasaurus* (Laaß 2014). Consequently, the quadrate process lies almost freely in a shallow groove of the squamosal and the paroccipital process (Barry 1967) and forms as in other non-mammalian synapsids a "ball and socket joint" (Laaß 2014; Luo and Crompton 1994; Kemp 1969) (Fig. 2D, E).

Medially, the contact facets of the stapedial head and the quadrate ramus of the pterygoid are visible as slight impressions at the quadrate (Fig. 5B). As in other non-mammalian synapsids the ventral part of the quadrate, the trochlea, bears the medial and the lateral articular condyles, which are separated by a deep trochlear trough from each other.

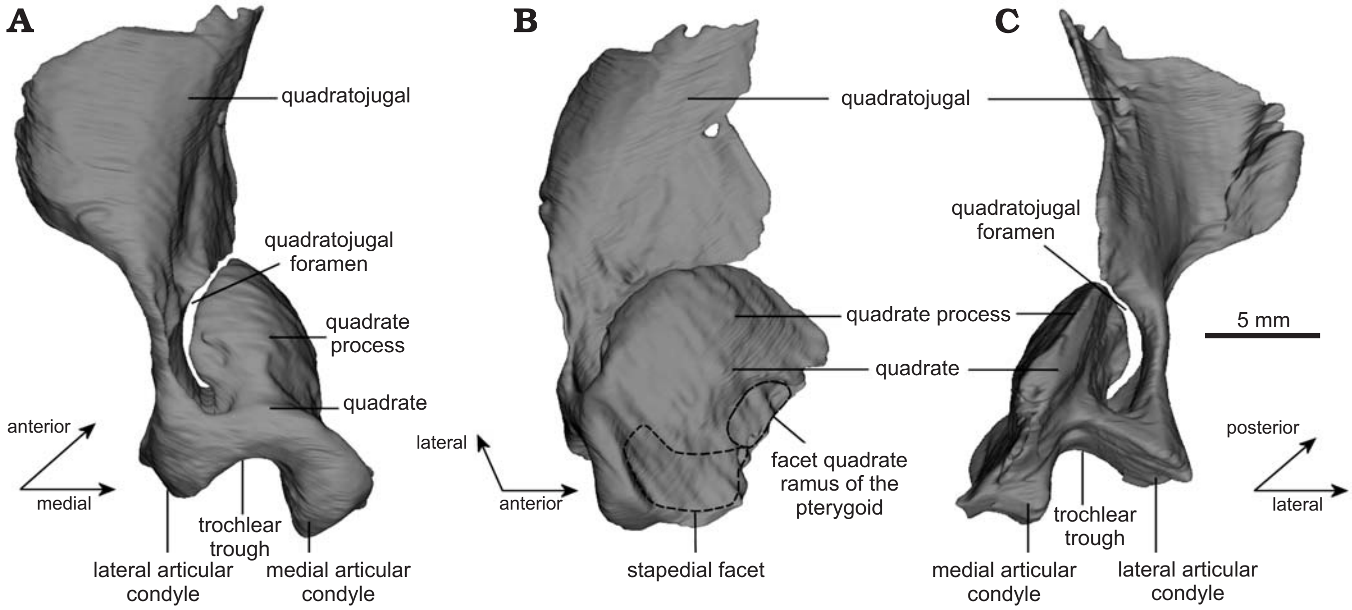

Fig. 5. Virtual reconstruction of the left quadrate-quadratojugal complex of the non-mammalian synapsid *Pristerodon mackayi* Huxley, 1868 (MB.R.985) from the Late Permian of Biesjespoort, South Africa; in ventral (**A**), medial (**B**), and anterior (**C**) views.

A striking feature of *Pristerodon*, which has also been observed by Keyser (1993), is the ventral expansion of the medial articular condyle. Its lateral side provides a large, dorsoventrally orientated flat contact surface with the articular condyle of the mandible (Fig. 5A, C).

The quadratojugal is the only portion of the quadratojugal complex which is dorsally fused with the cranium. Ventrally, it is a thin sheet of bone, but dorsally it becomes wider and slighly scrolled.

Description of the mandible.—The mandible of MB.R.985 does not strikingly differ from the well-known anatomy of *Pristerodon* (Barry 1967; Keyser 1993; King and Rubidge 1993). It also consists of a tooth-bearing dentary portion, i.e., the dentary and the splenial, and the accessory (postdentary) bones, which are the surangular, angular and the fused articular and prearticular, respectively (Fig. 6). The dentary bears 8–9 teeth on each side of the mandible, whereas two or three of them are small unerupted teeth and situated medially from the larger teeth.

In MB.R.985 medial and lateral flanges of the surangular as well as most parts of the reflected lamina are absent. However, two other specimens of *Pristerodon* (SAM-PK-K1658 and SAM-PK-10153) as well as the specimen figured by King and Rubidge (1993: 137) shows that the reflected lamina was greatly enlarged and had an almost circular shape (SOM 1: figs. S1, S2). Consequently, the area of the reflected lamina in MB.R.985 originally had a diameter of about 14 mm, which amounts to an area of about 154 mm^2. In both specimens SAM-PK-K1658 and SAM-PK-10153 the reflected lamina is almost completely preserved. It shows an anteroposteriorly oriented ridge or flexure, which divides this structure into a dorsal and a ventral portion. Furthermore, a flexure runs in both specimens from the median ridge to the ventral rim of the reflected lamina (SOM 1: figs. S1, S2).

Neutron tomography reveals that the postdentary bones are deeply inserted into the dentary, but not sutured with it, which indicates that they were only attached by soft tissue to the dentary (Fig. 6B–D). A similar morphology has also been described for the dicynodont *Eosimops* by Angielczyk and Rubidge (2013).

Acoustic function of the sound conducting apparatus.—As previously mentioned the stapes of *Pristerodon* was not fused with the cranium and in loose contact with the fenestra vestibuli and the medial side of the quadrate process. Although, no stapedial process could be observed, it seems likely that the stapes was connected by soft tissue ligaments to the cranium during life and probably surrounded by an air-filled cavity. A hint for a tympanic cavity around the stapes might be the system of cavities in the prootic and the opisthotic (Fig. 3), which are ossified from the embryonic otic capsule in the extant amniotes (De Beer 1937), which might represent extensions of the middle ear cavity into the surrounding bones such as the mastoid cells of mammals. Intramural sinuses have also been described for the docodont *Haldanodon exspectatus* (Ruf et al. 2013). The function of intramural sinuses is obscure, but it seems that they were probably related to low-frequency hearing and a fossorial mode of life (Witmer 1997; Ruf et al. 2013). Other possible functions of tympanic recesses may be the acoustical isolation of the auditory apparatus from self-generated sounds, pressure equalization on either side of the tympanum, localization of sounds, shock absorption, weight reduction, thermal insulation of the CNS as well as structural functions (for an overview see Witmer 1997). As it seems difficult to identify pneumatic foramina in *Pristerodon*, their

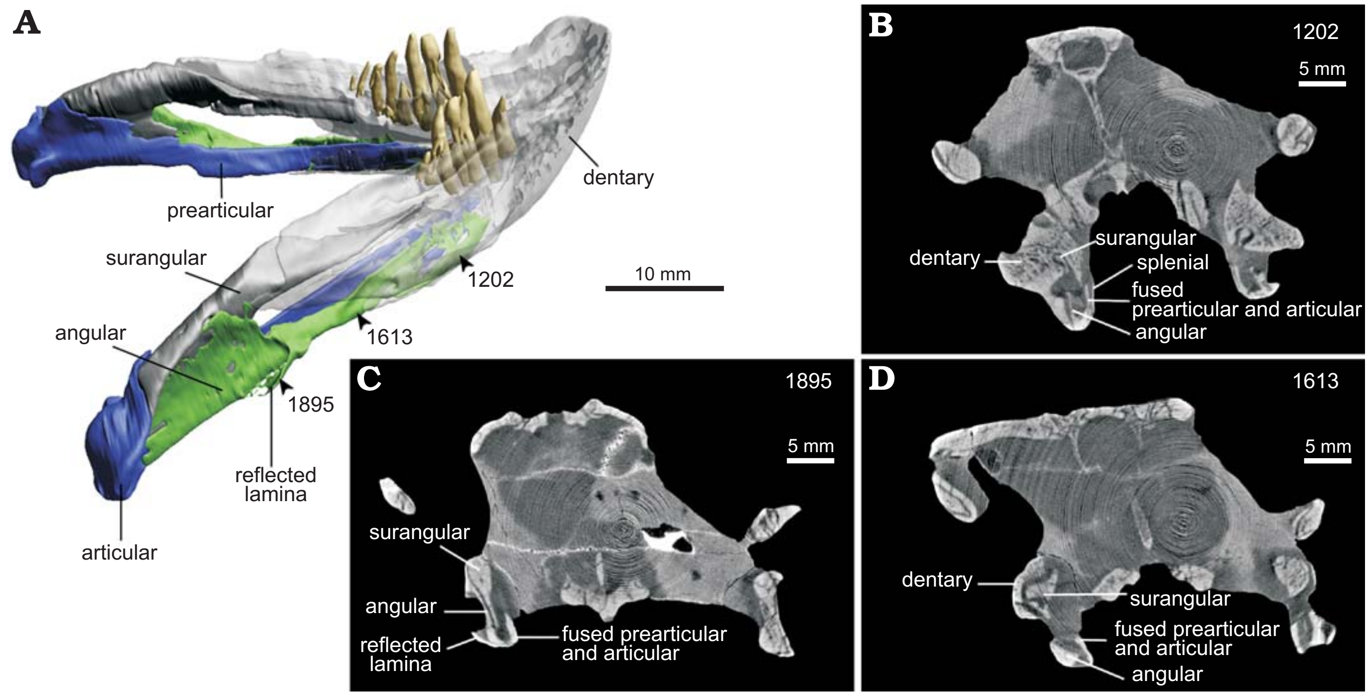

Fig. 6. The mandible of the non-mammalian synapsid *Pristerodon mackayi* Huxley, 1868 (MB.R.985) from the Late Permian of Biesjespoort, South Africa. **A**. Virtual reconstruction from neutron tomographic data. Note that the dentary is shown in transparent to provide insight into the internal structure. The arrows mark the positions and the number of the tomographic slices shown in B–D. **B**–**D**. Tomographic slices (**B**, 1202; **C**, 1895; **D**, 1613) showing the internal structure of the mandible. Note that surangular, prearticular, and angular are not fused with the dentary.

pneumatic nature is uncertain. In any case, the horizontal orientation of the stapes suggests that they did not have any structural function in the cranium and predominantly served for sound transmission (Clack 1997, 2002). This is probably supported by the sloped contact facet between the distal end of the stapes and the quadrate. In case of laterally applied forces the stapes was probably able to slip slightly along the surface of the quadrate process, which might have prevented the destruction of the delicate inner ear structure. Thus, it seems more likely that laterally applied forces from the mandible were braced by the quadrate ramus of the pterygoid rather than by the stapes.

As the quadrate process and the quadratojugal were dorsally not in contact or fused together, but separated from each other by a narrow deep cleft, the quadrate process lies almost free in the shallow groove formed by the squamosal and the paroccipital process. One exception is a small sutural connection with the base of the quadratojugal, which is in turn dorsally fused with the cranium. As a consequence, the stiffness of the quadrate process was certainly relatively high in comparison to the stapes. Nevertheless, the only reasonable explanation for the peculiar anatomy of the quadrate-quadratojugal complex is that the quadrate process served for both transmission of sound from the mandible to the stapes and to withstand the forces from feeding (see Fig. 7). Certainly, hearing was only possible when the masticatory musculature was relaxed. Only in this case was the quadrate moveable and able to transmit vibrations from the articular to the stapes. Conversely, hearing was certainly impossible for short periods during mastication. Then the quadrate process was pressed against the quadratojugal and the cleft between them became closed (Fig. 7). The fixation of the quadrate may have also been a protective mechanism for the delicate inner ear against stress and extreme "noise" from feeding (Albrecht Eiber, personal communication 2014). Similar mechanisms to protect the inner ear against high noise levels are also known for the mammalian middle ear, i.e., the middle ear muscles contract and stiffen the ossicular chain to decrease the efficiency of sound transmission and sound amplitudes (Fleischer 1978: 48).

It should be mentioned that King (1981) also assumed small movements of the quadrate-quadratojugal complex between quadratojugal and squamosal due to the fact that the quadratojugal is often not intensely fused with the cranium. Although this seems to be correct, it should be taken into consideration that the quadratojugal widens substancially dorsally and is scrolled in transverse section. Consequently, movements of the quadrate-quadratojugal complex in the lateral direction are mechanically obstructed despite its poor co-ossification with the squamosal. It is, therefore, more likely that lateral movements took place near the suture of the quadratojugal and the quadrate, which is the narrowest and thinnest region.

The question of what was the area for sound detection and which possible routes for sound transmission existed should be discussed. In general, two putative routes of sound transmission from the mandible seem to be possible, the "seismic" route from the ground to the jaw hinge and the "tympanic" route from the reflected lamina to the jaw

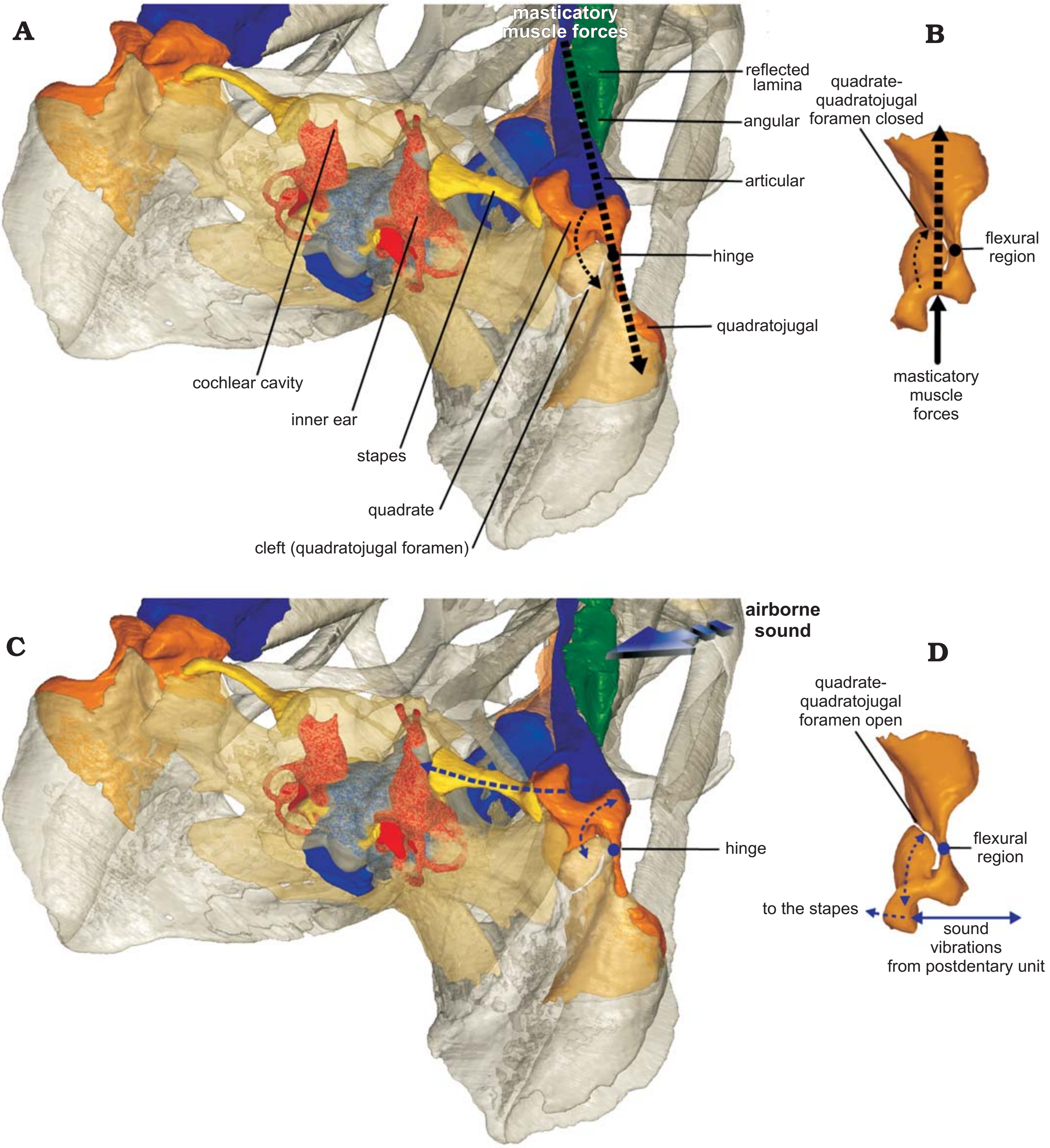

Fig. 7. Dual function of the auditory and masticatory apparatus of the non-mammalian synapsid *Pristerodon mackayi* Huxley, 1868 (MB.R.985) from the Late Permian of Biesjespoort, South Africa. **A**. Auditory region in posteroventral view showing the mechanics of the jaw articulations during mastication. **B**. Masticatory forces at the quadrate-quadratojugal complex (in posterior view). **C**. Auditory region in posteroventral view showing the mechanics of sound conduction. **D**. Mechanics of sound conduction of the quadrate-quadratojugal complex in posterior view. When the jaw muscles were relaxed, the reflected lamina and its putative tympanic membrane would receive the airborne sound, which would cause medio-lateral vibrations of the postdentary bones (although in small amplitude). The sound vibration was transmitted via the jaw hinge and the horizontal stapes to the inner ear. During the vibration, the quadrate is mobile at its ball and socket joint to the cranium, as permitted by a very thin bony connection with the quadratojugal. However, when the jaw musculature contracted during mastication, the quadrate was immobilized, it was strained by masticatory force and oppressed against the quadratojugal and the cleft between the quadrate and the quadratojugal is closed. During the active mastication, hearing was likely suspended, or reduced to a very low sensitivity if feasible at all. Not to scale.

articulation. Seismic sound, if at all, could only be perceived from the ventral side of the mandible, because the upper jaw and the tusks prevented pressing of the lateral side of the mandible against the substrate. But, due to the horizontal oriented stapes (Fig. 7), the content of sound transmitted from the ground F_g was negligible ($F_g \times \sin 90° \approx 0\%$), because the direction of seismic sound detected with the mandible was almost perpendicular to the long axis of the stapes (Laaß 2014). However, in real life seismic sound may have still caused small rocking motions of the stapes due to the coupling of the stapes by soft-tissue ligaments to the quadrate. The same seems to be true for stress of the mandible from feeding, which was predominantly dorsoventrally and rostrocaudally orientated, because the masticatory cycle of the mandible of dicynodonts comprised not only forward-backward movement but also dorso-ventral movement (Crompton and Hotton 1967). Lateral movements of the mandible were only small, because they were restricted by the specialized anatomy of the jaw articulation and the distance of the tusks (Crompton and Hotton 1967). Consequently, only a small content of the stress from feeding was transmitted to the stapes (Fig. 7). Therefore, it can be concluded that the middle ear of *Pristerodon* was inefficient to transmit seismic sound and stress from feeding to the inner ear in contrast to the ears of *Kawingasaurus* (Laaß 2014) and other anomodonts having lateroventral oriented stapes (Fig. 8).

In contrast, sound from the lateral side of the mandible could be transmitted more efficiently by piston-like movements of the stapes to the inner ear. Ignoring dampening of sound, theoretically a content of $F_a \times \cos 90° \approx 100\%$ of sound from the lateral side of the mandible could be transmitted to the inner ear (Laaß 2014). Thereby, the enlarged medial trochlear condyle might have been useful for sound transmission, because it provided a large dorsoventrally oriented contact facet to the articular condyle of the mandible (Fig. 7). A further argument for an efficient tympanic route is the fact that none of the postdentary bones was fused with the dentary as it has been also reported for advanced cynodonts (Kemp 2007). Acoustically isolation of the ear region has also been described for mammals (Fleischer 1978). Consequently, the postdentary unit was partially acoustically isolated from the rest of the mandible and able to vibrate more independently from the dentary. Thus, the postdentary units of *Pristerodon* represented two *de facto* acoustically independent sound receivers as the two sides of the mandible of some snakes, which is crucial for sound localisation (Friedel et al. 2008; Köppl 2009). A further consequence was that bone conduction in the mandible was obstructed by the discontinuities between the dentary and the postdentary bones.

Remarkably, there is evidence of a connection between the ceratohyal and the stapes in *Lystrosaurus* (Barry 1968; Cluver 1971). Barry (1968: pl. 15: B) figured a specimen showing the ceratohyal, which is situated ventrally at the lateral (distal) end of the stapes. Nevertheless, Barry (1968) as well as Cluver (1971) came to the conclusion that the ceratohyal was in all probability attached medially, because they could observe there a small facet on the ventral side of the stapes. Unfortunately, there is no sign for a facet on the stapes of *Pristerodon*, which might be a hint for the attachment of the ceratohyal. If a connection between the stapes, the hyoid apparatus and the mandible in *Pristerodon* also existed, which seems reasonable, this might be a further possible pathway for sound conduction from the mandible to the stapes.

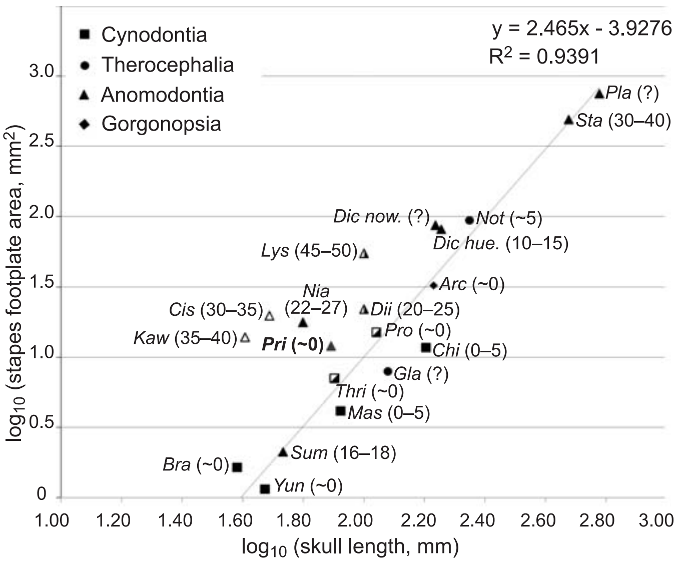

Fig. 8. Relative size of the stapes footplate area of the non-mammalian synapsid *Pristerodon mackayi* (MB.R.985) from the Late Permian of Biesjespoort, South Africa compared with those of other non-mammalian synapsids. The slope of the stapes for each taxon is added in brackets. The regression line is calculated only for non-fossorial species. Note that the stapes footplate area of *Pristerodon* is smaller than in fossorial taxa. Used data and material see SOM 1: table S2. Abbreviations: hollow symbols, fossorial species; partially filled symbols, semifossorial; filled symbols, non-fossorial or uncertain species; Arc, *Arctognathus nasuta*; Bra, *Brasilitherium riograndensis*; Chi, *Chiniquodon theotenicus*; Cis, *Cistecephalus planiceps*; Dic hue, *Dicynodon huenei*; Dic now, *Dicynodontoides nowacki*; Dii, *Diictodon feliceps*; Gla, *Glanosuchus* sp.; Lys, *Lystrosaurus declivis*; Mas, *Massetognathus pascuali*; Nia, *Niassodon mfumukasi*; Not, *Nothosollasia lückhoffi*; Pri, *Pristerodon* sp.; Pla, *Placerias gigas*; Pro, *Procynosuchus delaharpeae*; Sta, *Stahleckeria potens*; Sum, *Suminia getmanovi*; Thri, *Thrinaxodon liorhinus*; Yun, *Yunnanodon*. Modified from Laaß (2014).

Altogether, the results suggest that the ear of *Pristerodon* was rather sensitive to airborne sound, which was detected with a tympanum at the lateral side of the mandible, rather than to the detection of seismic sound from the ground.

Indeed, if a route for transmission of airborne sound from the lateral side of the mandible via the jaw articulation existed in *Pristerodon*, one can expect a specialized anatomical structure for detection of airborne sound in this region. A possible structure for sound detection might be the reflected lamina (Allin 1975; Allin and Hopson 1992; Maier and van den Heever 2002), which has been alternatively interpreted as an area for insertion of the jaw musculature (Janensch 1952; Hopson and Barghusen 1986; King 1981; Kemp 2007).

Muscle attachment at the reflected lamina, if at all, was certainly only possible in basal therapsids, which had massive reflected laminae that were able to withstand the forces of the jaw musculature. However, the reflected laminae of most advanced non-mammalian synapsids tend to became larger and thinner (Allin 1986) and were in some cases only 0.1–0.5 mm thick (Maier and van den Heever 2002). It is very unlikely that such a delicate structure served as an area for muscle attachment. As previously mentioned, the reflected lamina of *Pristerodon* was also a strikingly large structure and relatively thin. In MB.R. 985 the proximal part of the reflected lamina is 0.3–0.5 mm thick.

It should be noted that the reflected lamina represents a well-known acoustical element, a panel absorber (Everest and Pohlmann 2009), which is used as a device for sound absorption in concert halls and elsewhere. A panel absorber consists of a panel or a stiff membrane, which is able to vibrate and ideally covers an air-filled cavity. The air cushion interacts with the panel in a similar manner as a spring. Particularly, sound at lower frequencies can be effectively absorbed by a panel absorber mainly of its natural (resonant) frequency, which depends on the surface density of the panel and the depth of the air cavity behind it (Everest and Pohlmann 2009):

$$f = \frac{600}{\sqrt{(d \cdot m)}}$$

where: f, frequency of resonance of the panel (Hz); d, depth of airspace behind the panel (cm); m, surface density of panel or membrane (kg/m^2).

For example, a 1 mm thick bony plate having a density of 2 g/cm^3 amounts to a specific mass of 2 kg/m^2. For comparison, a similar plate, which is only 0.1 mm thick, would have a specific mass of 0.2 kg/m^2, respectively. If each panel would cover a 3 mm thick air cushion, their natural frequencies would be 770 Hz and 2.4 KHz, respectively, which corresponds to the frequency range of vocal communication of most animals. This example also shows that the limited bandwidth of a panel absorber can be enhanced by variations in the thickness of the panel and/or by variations in the thickness of the air cushion behind it. In fact, the reflected laminae of therapsids are proximally thicker and become distally extremely thin, which may be an indication for an increased sensitivity to a wide range of low-frequencies. An estimation of the frequency range of the reflected lamina and mandibular recess on the basis of a three dimensional virtual reconstruction of a well preserved specimen of *Pristerodon* will be subject of a future study.

If a connection of the mandibular recess with the mouth cavity existed (Allin and Hopson 1992), the depth of the air cushion would be further increased resulting in an enhanced sensitivity towards low frequencies. Another consequence of an air connection via the mouth cavity would be acoustically coupled reflected laminae or eardrums, which enable animals to localise sound sources according to the mechanism of pressure difference receivers (Köppl 2009). Interestingly, this is the only known mechanism which enables animals with small interaural distances to localise low-frequency sound (Köppl 2009).

The ability of the therapsid mandibular ear to conduct airborne sound has been questioned, because of the large masses of the middle ear bones and dampening effects of sound by soft tissue ligaments (King 1981; Kemp 2007). Although the density of bone in *Pristerodon* cannot be determined exactly, it seems reasonable that the combined mass of the middle ear bones of *Pristerodon* was about 2–3 times as large as those of an elephant, which has a combined mass of the ear ossicles of 650 mg (Reuter et al. 1998). However, the high frequency limit of the middle ear depends on the mass of the bones and their inertia (Hemilä et al. 1995). Consequently, the middle ear of elephants is only restricted to low-frequency sound with best sensitivity at 1000 Hz (Hemilä et al. 1995). It seems, therefore, reasonable that *Pristerodon* was probably able to hear low-frequency air-borne sound in the range lower than 1 KHz. In comparison to other dicynodonts, *Pristerodon* was small-sized and also possessed middle ear bones towards the lower end of the size spectrum of other dicynodonts.

Remarkably, it has been demonstrated for modern snakes that weak sound waves lower than 1 KHz can be transmitted very efficiently via soft-tissue ligaments from the mandible via the jaw articulation to the inner ear, which might be explained with the stiffening effect (Friedel et al. 2008; Thomsen 2003).

Indeed, if *Pristerodon* possessed an airborne-sound sensitive ear, it must have been able to amplify sound. The sound pressure transformer ratio can be roughly estimated from the area ratio of the tympanic membrane and the stapes footplate (Maier and van den Heever 2002; Kemp 2007). As previously noted, the reflected lamina in MB.R.985 had an area of about 154 mm^2, the stapes footplate area is about 12 mm^2, which gives a sound pressure tranformer ratio of approximately 13. Compared with the sound pressure transformer ratio of mammals, which ranges between 10 and 40 (Rosowski and Graybeal 1991; Rosowski 1992), an impedance matching of 13 is relatively small, but significantly larger than the low impedance matching of 2–3 for the fossorial anomodont *Kawingasaurus* (Laaß 2014). Interestingly, modern ground-dwelling mammals also tend to have smaller stapes footplates than fossorial taxa (Mason 2001), which supports the hypothesis of an enhanced sensitivity to airborne sound and a non-fossorial lifestyle or at least a large extent of surface activity for *Pristerodon*.

Relationship between hearing, lifestyle, and posture.—The question arises, which selective pressures might have triggered the origin of tympanic hearing in synapsids? The ability to hear airborne sound has numerous advantages for animals to detect danger or prey, to communicate with conspecifics or to warn other animals using sound (Manley 2010). This might be particularly crucial for ground dwelling animals, which were not able to take shelter in a burrow.

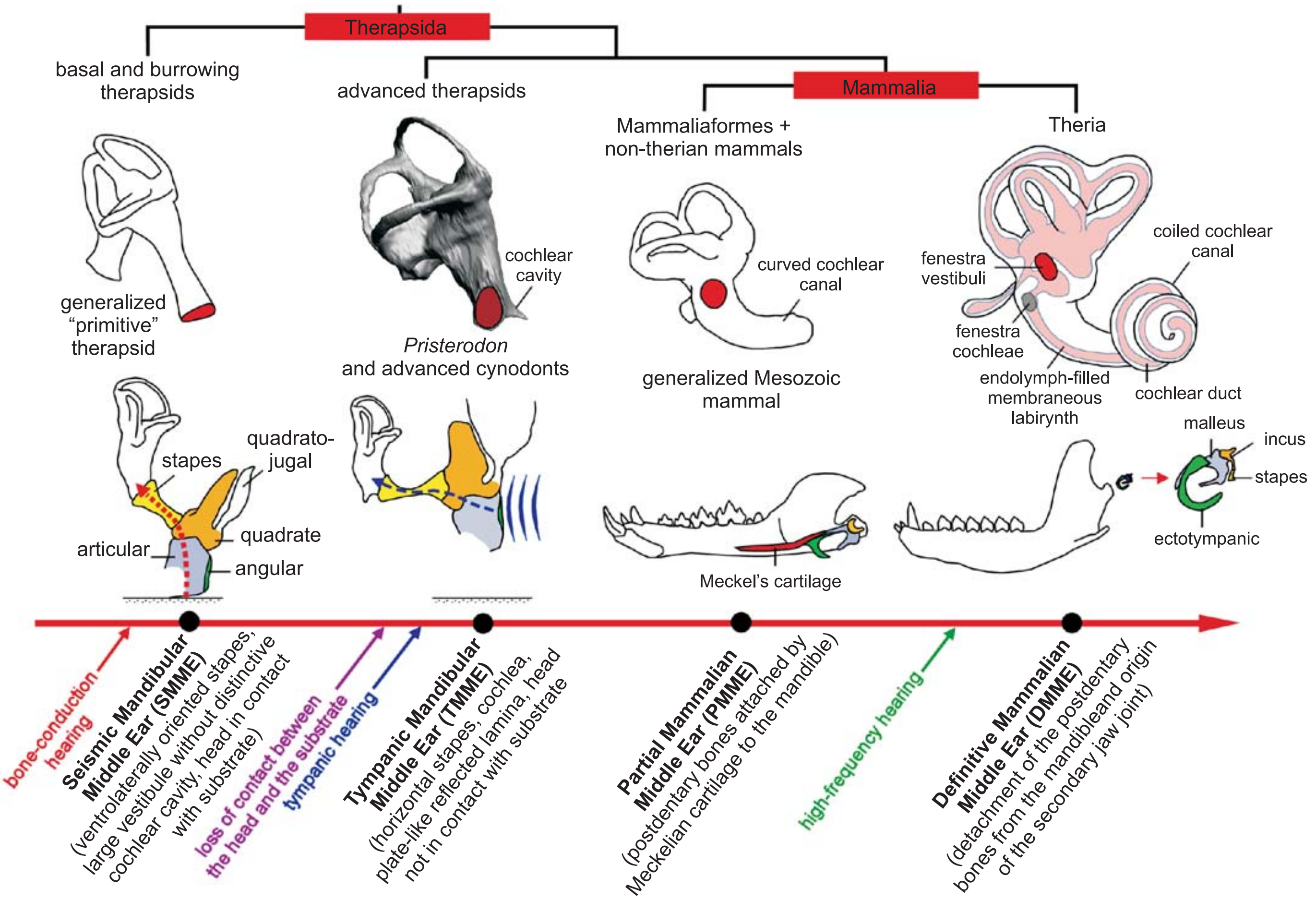

Fig. 9. Co-evolution of the cochlea and middle ear in synapsids. Hearing in primitive or burrowing non-mammalian synapsids was predominantly by bone conduction from the ground vibration via the mandible. The tympanic hearing started to assume a more important role as the head became lifted from ground due to a more upright forelimb posture. Adaptations to tympanic hearing and modifications of the middle ear for better sensitivity to airborne sound include: an enhanced acoustical isolation of the postdentary bones from the dentary, an enlarged reflected lamina, a smaller stapes footplates and a more horizontal oriented stapes, an elongate medial trochlear condyle of the quadrate. All these coincided with the origin of a distinctive cochlear cavity. Concurrent with middle ear modifications, the inner ear developed a more laterally facing fenestra vestibule and a ventral cochlear cavity. Later, the detachment of the postdentary bones from the mandible and the elongation of the cochlear canal were further steps towards a refined sensitivity to airborne sound, especially in higher frequencies. Partially redrawn from Luo et al. (2011), Cox (1962), and Luo (2011).

The postcranial anatomy of dicynodonts suggests that burrowing was to various degrees part of their behaviour regime (Ray and Chinsamy 2003; Ray 2006; Kümmell 2009). For instance, *Kawingasaurus* and *Cistecephalus* clearly show several adaptations to a fossorial lifestyle (Cox 1972; Cluver 1978; Nasterlack et al. 2012; Laaß 2014). *Lystrosaurus* and *Diictodon* were more generalized dicynodonts, but were found in burrows, which is also an indication for a burrowing behaviour (Smith 1987; King and Cluver 1991; Groenewald 1991; Ray and Chinsamy 2003; Retallack et al. 2003; Ray 2006; Kümmell 2009). The condition in *Niassodon* is uncertain, because most parts of the forelimb skeleton are not preserved (Castanhinha et al. 2013).

Little is known about the lifestyle of *Pristerodon*, but there is no evidence for a burrowing behaviour (Ray and Chinsamy 2003; Ray 2006), which would result in a closer contact between the skull and the substrate. This might also be supported by the relatively small stapes footplate as mentioned above. A comparison of the postcranium of *Pristerodon* with those of the basal dicynodonts *Eodicynodon* and *Robertia* revealed several modifications towards a more upright posture of the forelimbs such as caudolaterally orientated gleno-humeral and acetabular articulations (Ray and Chinsamy 2003; Ray 2006). Although *Pristerodon* also had abducted humeri and a semi-erect posture (Ray and Chinsamy 2003; Ray 2006), these results suggest that *Pristerodon* probably more frequently hold its head above the ground than primitive taxa. If so, the detection of seismic sound by bone-conduction via the head was not so important for this animal. Otherwise, the loss of contact between the head and ground would necessitate that the tympanic middle ear develop an impedance matching for better reception of airborne sound (Tumarkin 1955, 1968; Kermack and Mussett 1983; Kermack and Kermack 1984). Consequently, the current data about lifestyle and posture support the hypothesis of an enhanced sensitivity to airborne sound for *Pristerodon*.

Discussion and conclusions

As described above, the middle ear of *Pristerodon* with a horizontal oriented stapes seems to be better suited to hear airborne sound. A more horizontal orientation of the stapes is also known for most therocephalians, cynodonts and mammaliaformes (Fig. 8). In contrast, pelycosaurs, primitive therapsids as well as fossorial taxa such as *Kawingasaurus* and *Cistecephalus* or semifossorial taxa such as *Lystrosaurus* and *Diictodon* have ventrolaterally oriented stapes and it seems that this feature is correlated with enlarged stapes footplates (Fig. 8), which might be an indication for seismic sensitivity (Mason 2001; Laaß 2014).

It should be taken into consideration that the ears of different therapsid clades probably show group-specific characteristics. For example, it seems that the middle ear bones of anomodonts tend to be generally larger than those of theriodonts and, as already previously noted, their postdentary bones show an evolutionary trend to become larger in contrast to theriodonts (Sidor 2003). Consequently, the most reliable information about a possible influence of fossoriality on the dimensions of the stapes footplate area arises from comparisons of taxa within the same clade in Fig. 8.

However, the differences in the middle ear anatomy between primitive or fossorial and non-fossorial therapsids might reflect a change of the route of sound perception from the ventral route of the mandible to the lateral side of the mandible, presumably for detecting seismic vibration, and airborne sound, respectively (Fig. 9).

Obviously, the described differences in the middle ear anatomy of *Pristerodon* in comparison to fossorial species are also reflected in the gross anatomy of the inner ear. Especially, the horizontal oriented stapes required a curved vestibule and a rotation of the fenestra vestibuli to a lateral position to accomodate the stapes footplate in the fenestra vestibuli. Remarkably, the free space in the basioccipital ventrally from the vestibule was occupied by a small cochlea, which might be an indication for an elongated basilar papilla, which was probably able to sense an increased range of sound frequencies. As previously mentioned, small cochlear cavities are also known for some advanced cynodonts with horizontal oriented stapes such as *Brasilitherium* and *Massetognathus* (Fig. 8), but unknown for fossorial anomodonts with steeply sloped stapes (Fig. 8). An intermediate position is represented by *Niassodon*, which had a slightly inclined stapes with a relatively large footplate and a short cochlea (Fig. 8). It should be noted that *Pristerodon* is not a direct ancestor of mammals, but its inner ear anatomy resembles those of some advanced cynodonts and represents a connecting link between the primitive therapsid inner ear condition and the mammalian inner ear, which also has the fenestra vestibuli at the lateral side of the vestibule and a cochlea ventrally (Fig. 9).

It appears that the described differences of the middle and inner ear anatomy of therapsids were closely related to the lifestyle and forelimb posture, i. e. the extent of contact between the head (mandible) and the substrate. Due to the relevance of these different ear types with respect to the origin of tympanic hearing, it is proposed here to distinguish the dual function between the Seismic Mandibular Middle Ear (SMME) and the Tympanic Mandibular Middle Ear (TMME) of therapsids, respectively for receiving ground-transmitted sound, and for receiving airborne sound (Fig. 9).

The results of this study suggest that *Pristerodon* was probably one of the earliest synapsids, which was able to hear airborne sound and show that inner ears with distinctive cochlear cavity and an impedance matching middle ear already evolved at least in some basal therapsids of the Late Permian. Consequently, tympanic hearing in synapsids originated even before the postdentary bones detached from the mandible and a secondary jaw articulation evolved. Obviously, this key evolutionary event was coincided with changes in the postcranium towards a more upright stance in ground-dwelling therapsids.

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