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3D atlas and comparative osteology of the middle ear ossicles among Eulipotyphla (Mammalia, Placentalia).

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Abstract

Considerable morphological variations are found in the middle ear among mammals. Here I present a three-dimensional atlas of the middle ear ossicles of eulipotyphlan mammals. This group has radiated into various environments as terrestrial, aquatic, and subterranean habitats independently in multiple lineages. Therefore, eulipotyphlans are an ideal group to explore the form-function relationship of the middle ear ossicles. This comparative atlas of hedgehogs, true shrews, water shrews, mole shrews, true moles, and shrew moles encourages future studies of the middle ear morphology of this diverse group.

Keywords: aquatic adaptation, convergence, Eulipotyphla, fossorial adaptation, hearing

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INTRODUCTION

The middle ear ossicles in the mammalian ear play an essential role in impedance matching and transmitting airborne sounds from the tympanic membrane to the inner ear (Lavender et al., 2011; Solntseva, 2011). In theory, the morphology of the middle ear ossicles is assumed to be related to ecological peculiarities of each species (Mason, 2016). Some mammals which secondarily shifted their habitats from terrestrial environment have been required to alter their auditory mechanisms. This is because the media which propagate sounds and sound prevalent frequencies differ from terrestrial environment (Aitkin et al., 1982; Ketten, 1992; Nummela, 1995, Nummela et al., 1999). For example, true seals are equipped with extraordinary large ossicles to hear airborne sounds both in air and water (Nummela, 1995; Nummela et al., 1999). Relatively long manubriums are found in the middle ear ossicles of bats to hear ultrasonic sounds (Henson Jr, 1961).

Improvements of non-visual sensory organs are critical to live in the darkness where available light is limited. Previous studies have identified that subterranean mammals tend to exhibit larger tympanic membrane, larger stapes footplate, loose connection between malleus and tympanic bone, and reduced middle ear muscles (Fleischer, 1978; Burda, 1979, 2006; Burda et al., 1990, 1992; Mason, 2001, 2003, 2006; Pleštilová et al., 2016; Wannaprasert, 2016). Their morphology is argued to be related to hearing low-frequency sounds and reduced impedance performance (Burda et al., 1990, 1992). Since low-frequency sounds are better propagated than high-frequency sounds in underground tunnels, subterranean eulipotyphlan moles use low-frequency sounds for vocalization (Heth et al., 1986).

Eulipotyphla (Gatesy, 2016) includes four families: Erinaceidae (hedgehogs and gymnures), Soricidae (shrews), Solenodontidae (solenodonts), and Talpidae (talpids). This group encompasses a wide range of ecological modes from semi-aquatic, subterranean, semi-subterranean to terrestrial lifestyle. Tenrecs, elephant shrews, and golden moles were once grouped together with Eulipotyphla as "Insectivora" (Asher et al., 2008). However, molecular evidence suggests that Eulipotyphla is a member of Laurasiatheria and that tenrecs, elephant shrews, and golden moles form Afrotheria, together with elephants, hyraxes, aardvarks, sireneans (Nishihara et al., 2009). The phylogenetic relationships among Eulipotyphla have been highly disputed but were recently clarified by molecular studies (Krettek et al., 1995; Ohdachi et al., 2001, 2004, 2006; Shinohara et al., 2003, 2004, 2005, 2014; Dubey et al., 2007; Bannikova et al., 2010; He et al., 2010, 2014). Among talpids, both morphological and molecular evidence supports that talpid common ancestor was not fully specialized for underground lifestyle and that further specializations for underground habits occurred independently in the Eurasian lineage (*Euroscaptor, Oreoscaptor, Mogera*, *Talpa*) and American lineage (*Scalopus, Scapanus, Parascalops,*) (Shinohara et al., 2003, 2014; Motokawa, 2004; Sánchez-Villagra et al., 2006).

Eulipotyphlans exhibit considerable variations in the middle ear ossicles. Doran (1878) conducted a comprehensive survey of the middle ear ossicles in mammals and commented that the eulipotyphlans "offer great variations in the different families of this order, and there is no constant positive character to be found in any of the three ossicula." The first comprehensive study of talpid middle ear ossicles was done by Stroganov (1945) with the aim of clarifying their phylogenetic relationships. Later, Henson Jr (1961) compared the middle ear morphology of *Erinaceus europaeus*, *Cryptotis parva*, and *Scalops aquaticus*. Variation and functionality of the middle ear ossicles of several eulipotyphlans have been investigated by Segall (1970), Mason (2001, 2006), Burda (1979), and

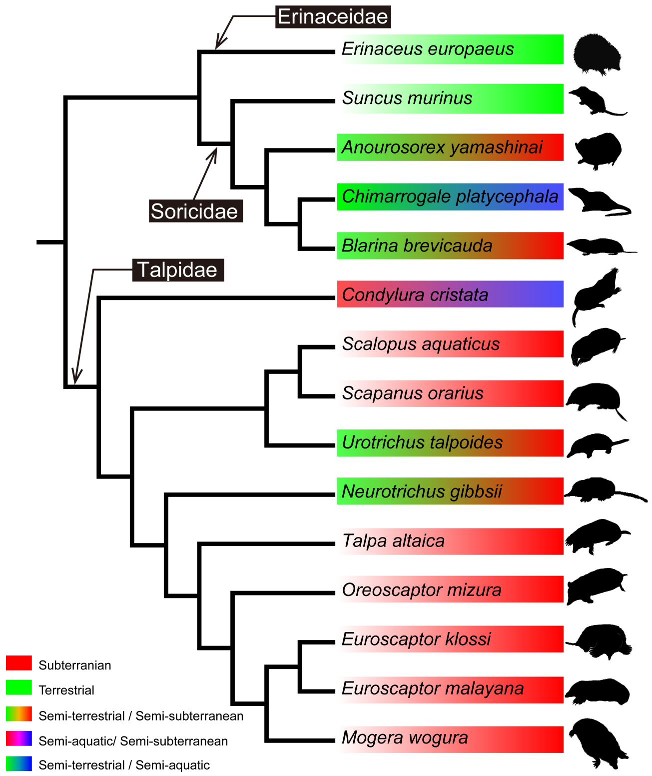


Figure 1. Phylogenetic relationships among the eulipotyphlan species and outgroups included in this study

Burda et al. (1992). However, most of these studies often compared highly subterranean talpids with phylogenetically distant taxa such as golden mole and mole rats to identify convergent patterns in the middle ear ossicles. Eulipotyphlans exhibit remarkable ecological variation, and their morphological diversity is accordingly predicted for auditory traits. However, comparisons of the middle ear ossicles within the group have hardly been conducted, due to their disputed phylogenetic relationships. The resolved phylogenetic relationships of eulipotyphlans now provide us with the framework to explore the evolution of the middle ear ossicles in this group.

Here I present an annotated three-dimensional atlas of the middle ear ossicles of eulipotyphlan mammals, which includes the first description for several species, to encourage future studies of middle ear morphology of this diverse group. Eulipotyphlan specimens curated at The University Museum of The University of Tokyo (Tokyo, Japan), and National Museum of Nature and Science (Tokyo, Japan) were scanned by microfocal X-ray CT system and reconstructed through manual segmentation. I provide a unique comparative atlas of hedgehogs, true moles, shrew moles, mole shrews, and shrews and briefly discuss the phylogenetic and ecological patterns of the middle ear ossicles.

METHODS

Specimens presented in this atlas are summarized in Table 1. All specimens used in this study have full teeth eruption and were considered as adults. The composite phylogenetic tree based on the full-length (1140bp) cytochrome *b* sequence data is given in Fig.1 (Krettek et al., 1995; Ohdachi et al., 2001, 2004, 2006; Shinohara et al., 2003, 2004, 2005; Dubey et al., 2007; He et al., 2010). Scan details and measurements are summarized in Table 1. Condylobasal length (CBL) of the skull was measured by calipers to the nearest 0.01 mm. Serial cross-sectional images were obtained by microfocal X-ray CT system of The University Museum, The University of Tokyo (TX225-Actis, Tesco Corporation). To obtain high resolution CT images, I conducted close-up scans of the left-side temporal bone region for each specimen. In case left side was destroyed, right side was scanned. Scanning parameters were 95 or 100kV tube voltage, 0.20mA tube current, and slice thickness and slice intervals were 12 to 34 μm. Cross-sectional images were reconstructed in a 512×512 matrix with pixel size equivalent to the slice interval/thickness, producing isotropic voxels. Defining the threshold between the CT values of bone and non-bone regions by half maximum height method (Spoor et al., 1993) using Amira 5.2 (Visage Imaging, Berlin, Germany), the bone boundaries of the middle ear ossicles were segmented with slice-by-slice manual adjustments.

DISCUSSION

Erinaceidae

Erinaceus europaeus

The overall shape of the middle ear ossicles (Fig.2) is more similar to that of soricids than to that of talpids. The anterior process of the malleus is robust and longer than the manubrium. An orbicular apophysis of the malleus is present, but it is not robust as those of soricids. The incus is rather small. The short process of the incus is round-shaped. The stapes is proportionally large, compared to the malleus and incus. The footplate of the stapes is flat and not wide.

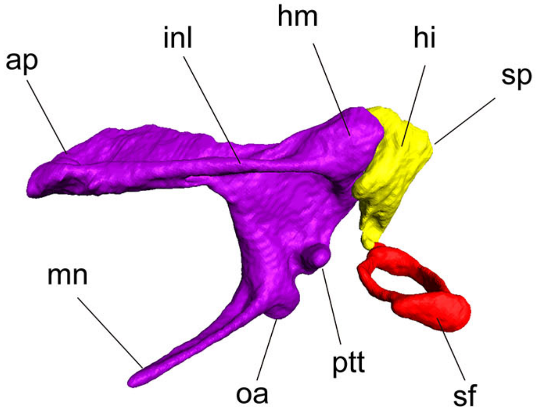
Soricidae

Anourosorex yamashinai

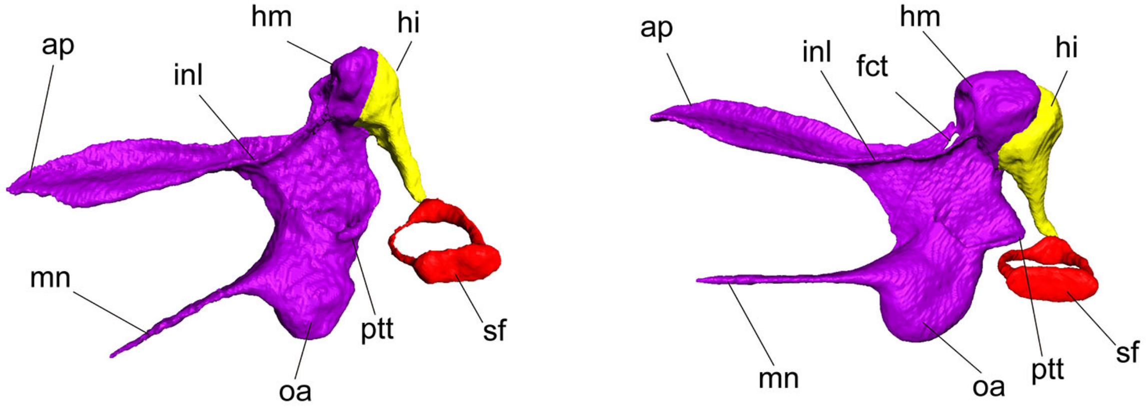
This Taiwanese mole shrew is a distinctive semi-subterreanean shrew endemic to Taiwan (Lin and Motokawa, 2014). The anterior process of the malleus is robust but just slightly longer than the manubrium (Fig.2). The manubrium is slender. An orbicular apophysis of the malleus is present, but it is not robust as that of the terrestrial *Suncus*. The incus is small. The short process of the incus is not evident and the incus head is rounded. The articulation between the malleus and incus is tight. The footplate of the stapes is flat and not wide.

Blarina brevicauda

This species has been treated as "non-fossorial" by Mason (2001), but it is actually known as the most subterranean among American shrews (George et al., 1986). The anterior process of the malleus is not robust, and slightly longer than the manubrium (Fig.2). The anterior process and the manubrium are both long and nearly parallel. A large foramen for chorda tympani is present on the neck of the malleus. The manubrium is slender. An orbicular apophysis of the malleus

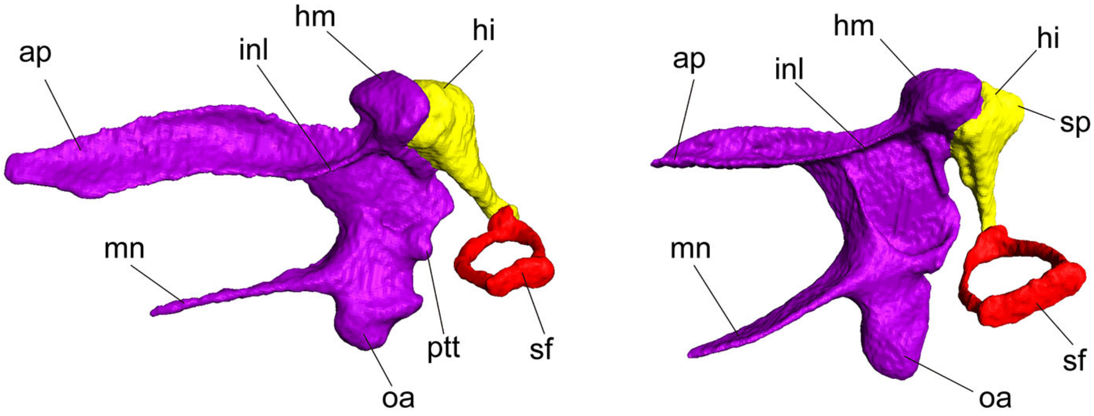


Erinaceus europaeus



Anourosorex yamashinai

Blarina brevicauda



Chimarrogale platycephala

Suncus murinus

Figure 2. Three-dimensional models of the middle ear ossicles of Erinaceidae (*Erinaceus europaeus*) and Soricidae (*Anourosorex yamashinai*, *Blarina brevicauda*, *Chimarrogale platycephala*, and *Suncus murinus*). Right-side middle ear ossicles are pictured from an internal view. The malleus is colored in purple, incus in yellow, and stapes in red. Abbreviations: ap, anterior process of malleus; fct, foramen for chorda tympani; hi, head of incus; hm, head of malleus; inl, inner lamella; mn, manubrium; oa, orbicular apophysis; ptt, muscular process for tensor tympani; sf, stapes footplate; sp, short process of incus.

Family	Species	Id	Coll.	Side	V.(kV)	Res. (µm)	CBL(mm)
Erinaceidae	*Erinaceus europaeus*	DK2331	UMUT	Left	95	28	51.45
Soricidae	*Anourosorex yamashinai*	SIK_yamashinai	NMNST	Left	100	16	20.66
	Blarina brevicauda	M8003	NMNST	Right	95	12	19.51
	Chimarrogale platycephala	DK5481	UMUT	Left	100	16	27.17
	Suncus murinus	DK1227	UMUT	Left	95	16	33.24
Talpidae	*Condylura cristata*	SIK0050	NMNST	Right	95	16	26.11
	Euroscaptor klossi	SIK0673	NMNST	Left	95	16	28.33
	Euroscaptor malayana	SIK_malayana	NMNST	Left	95	16	27.17
	Mogera wogura	DK2551	UMUT	Left	100	16	17.86
	Neurotrichus gibbsii	SIK_gibbsii	NMNST	Left	95	12	23.09
	Oreoscaptor mizura	DK6545	UMUT	Left	100	16	29.02
	Scalopus aquaticus	SIK_aquaticus	NMNST	Left	95	16	32.32
	Scapanus orarius	SIK_orarius	NMNST	Left	95	16	29.9
	Talpa altaica	SIK_altaica	NMNST	Right	95	16	33.34
	Urotrichus talpoides	DK0887	UMUT	Left	100	16	22.03

Table 1. List of specimens, repository institutions, CT data acquisition parameters and condylobasal length. All scans were performed using a current of 0.2 mA. Abbreviations: UMUT, The University Museum, The University of Tokyo; NMNST, National Museum of Nature and Science, Tokyo.

is present, but it is not strongly inflated as the terrestrial *Suncus*. The incus is rather enlarged. The short process of the incus is not evident and the incus head is rounded. The articulation between the malleus and incus is loose. The footplate of the stapes is flat and enlarged

Chimarrogale platycephala

This Japanese water shrew is a semi-aquatic shrew endemic to Japan (Ohdachi et al., 2009). It is distributed around mountain streams and is an obligate swimmer (Abe, 2003). The anterior process of the malleus is robust and slightly longer than the manubrium (Fig.2). The anterior process and manubrium are nearly parallel. The malleus body is rather slender and the head is small. An orbicular apophysis of the malleus is present, but it is not strongly inflated as in the terrestrial species *Suncus murinus*. The manubrium is slender. The short process of the incus is not evident and the incus head is round-shape. The articulation between the malleus and incus is loose. The footplate of the stapes is flat.

Suncus murinus

The length of the anterior process of the malleus is comparable to the manubrium (Fig.2). The malleus body is robust, and the head is large. An orbicular apophysis of the malleus is present, strongly inflated, and even larger than the head. The short process of the incus is round-shaped. The articulation between the malleus and incus is loose. The footplate of the stapes is enlarged and flat.

Talpidae

Condylura cristata

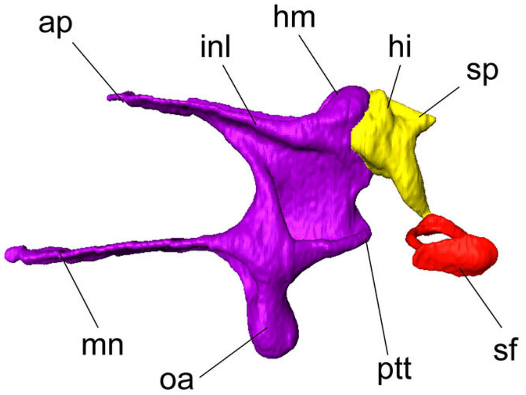
This species is a semi-aquatic / semi-subterranean talpid distributed in North America (Hamilton, 1931; Petersen and Yates, 1980). It can dig its tunnels but is not strongly fossorial as other American talpids such as *Scalopus* and *Scapanus* (Hamilton, 1931; Petersen and Yates, 1980). The anterior process of the malleus is considerably shorter than the manubrium (Fig.3), which appears to be a rare case among eulipotyphlans. The anterior process and manubrium are nearly parallel. The head of the malleus is small. An orbicular apophysis of the malleus is present and larger than the head of the malleus. The articulation between the malleus and the incus is loose. The footplate of the stapes is flat.

Euroscaptor klossi

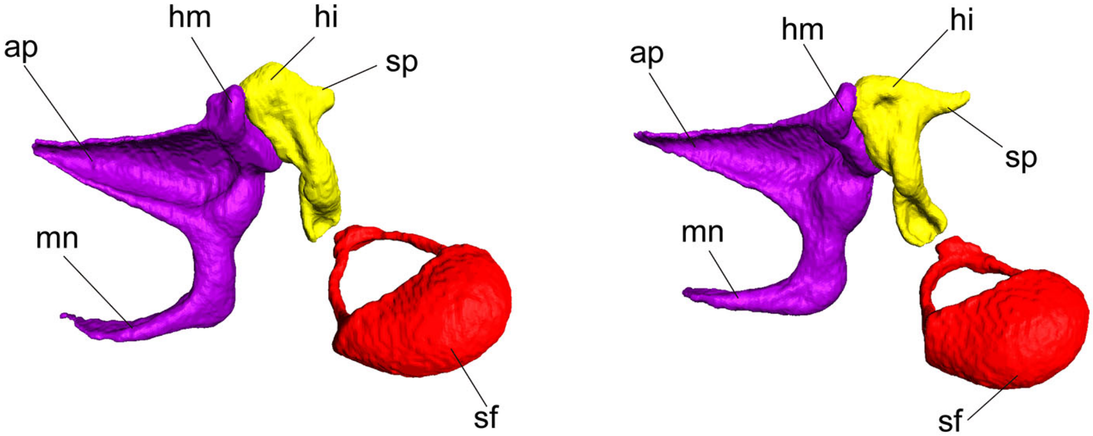
This is a Southeast Asian talpid (Miller, 1940; Kawada et al., 2003), whose ecology is not well known but presumably fully fossorial (Cassola, 2016). The anterior process of the malleus is not robust and similar in length with the manubrium (Fig.3). The anterior process and manubrium form a U-shaped curve, a characteristic trait of fully fossorial Eurasian talpids. An orbicular apophysis of the malleus is completely absent. The articulation between the malleus and incus is loose. The stapes is considerably enlarged, and even larger than the incus. The footplate of the stapes is inflated and rounded.

Euroscaptor malayana

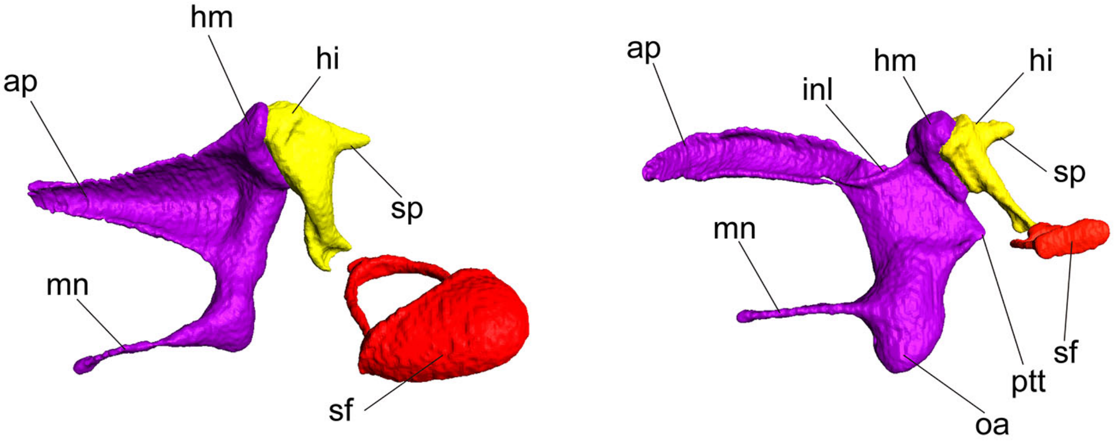
This Malaysian talpid is suggested to be closely related to *E. klossi* (Kawada et al., 2003; Shinohara et al., 2014). Still very little is known about its ecology (Kawada et al., 2003). It is presumably fully fossorial given its robust hand morphology and short tails, but it appears it prefers using surface tunnels and does not dig deeply into the ground (Kawada et al., 2003). The anterior process of the malleus is not robust and slightly longer than the manubrium, which is in contrast to *E. klossi* (Fig.3). The anterior process and manubrium form a U-shaped curve, similar to other fully fossorial Eurasian talpids. An orbicular apophysis of the malleus is completely absent. The articulation between the malleus and incus is loose. The incus is relatively larger than *E. klossi*. The short process of the



Condylura cristata



Euroscaptor klossi *Euroscaptor malayana*



Mogera wogura *Neurotrichus gibbsii*

Figure 3. Three-dimensional models of the middle ear ossicles of Talpidae (*Condylura cristata*, *Euroscaptor klossi*, *Euroscaptor malayana*, *Mogera wogura*, and *Neurotrichus gibbsii*)

incus protrudes much evidently than *E. klossi*. The stapes is larger than the incus as in *E. klossi*. The shape of the footplate is inflated and rounded.

Mogera wogura

This is a fully fossorial talpid found in Japan (Ohdachi et al., 2009). The anterior process of the malleus is not robust, and slightly longer than the manubrium (Fig.3). The anterior process and manubrium form a U-shaped curve as in other fossorial Eurasian talpids. An orbicular apophysis of the malleus is completely absent. The articulation between the malleus and incus is loose. The short process of the incus protrudes evidently. The stapes is considerably enlarged and larger than the incus. The footplate of the stapes is inflated and rounded.

Neurotrichus gibbsii

This American shrew mole is reported to be the least fossorial and smallest of the American talpids (Dalquest and Orcutt, 1942). The overall malleus shape is rather similar to soricids and erinaceids (Figs. 2, 3). The anterior process of the malleus is robust and longer than the manubrium. The anterior process and manubrium are nearly parallel and do not form a U-shaped curve. An orbicular apophysis of the malleus is absent as in soricids and erinaceids. The stapes and incus are proportionally smaller compared to the malleus, which is in contrast to fully fossorial Eurasian talpids and fully fossorial American talpids. The footplate of the stapes is thin and flat.

Oreoscaptor mizura

This species is a highly fossorial talpid endemic to Japan (Ohdachi et al., 2009). Recently, the nomenclature of the Japanese mountain mole *Euroscaptor mizura* was proposed to be revised as *Oreoscaptor mizura* (Kawada, 2016), given the molecular paraphyly of *Euroscaptor* and the distinctive morphology of *mizura*. The anterior process of the malleus is not robust (Fig.4). The manubrium is longer and more robust than the anterior process. This is not seen in *Euroscaptor* in which *O. mizura* was once classified. The anterior process and manubrium form a U-shaped curve as in other fossorial Eurasian talpids. The neck of the malleus is inflated, which differs from *Euroscaptor* and *Mogera*. An orbicular apophysis of the malleus is completely absent. The short process of the incus protrudes most remarkably among the studied eulipotyphlans. The stapes is considerably enlarged and larger than the incus. The footplate of the stapes is inflated and rounded.

Scalopus aquaticus

The anterior process of the malleus is not robust and is similar in length with the manubrium (Fig.4). The anterior process and manubrium are nearly parallel. The "lamina" (Stroganov, 1945) between the anterior process and the manubrium is thin. The head of the malleus is enlarged and similar in size with the head of the incus. The articulation between the malleus and incus is loose. An orbicular apophysis of the malleus is slightly present. The short process of the incus is present but small. Both the incus and stapes are proportionally enlarged. The footplate of the stapes is flat and not rounded as in *Mogera*, *Euroscaptor*, and *Oreoscaptor*.

Scapanus orarius

Overall shape of the middle ear ossicles is similar to that of *Scalopus* (Fig.4). The anterior process of the malleus is not robust and is similar in length with the manubrium. The anterior process and manubrium are nearly parallel. The "lamina" (Stroganov, 1945) between the anterior process and manubrium is thin and slightly enlarged than *Scalopus*. The head of the malleus is enlarged as in *Scalopus*. The articulation between the malleus and incus is loose. An orbicular apophysis of the malleus is slightly present. The short process of the incus is present. Both the incus and stapes are enlarged. The footplate of the stapes is flat and not rounded as in *Mogera*, *Euroscaptor*, and *Oreoscaptor*.

Talpa altaica

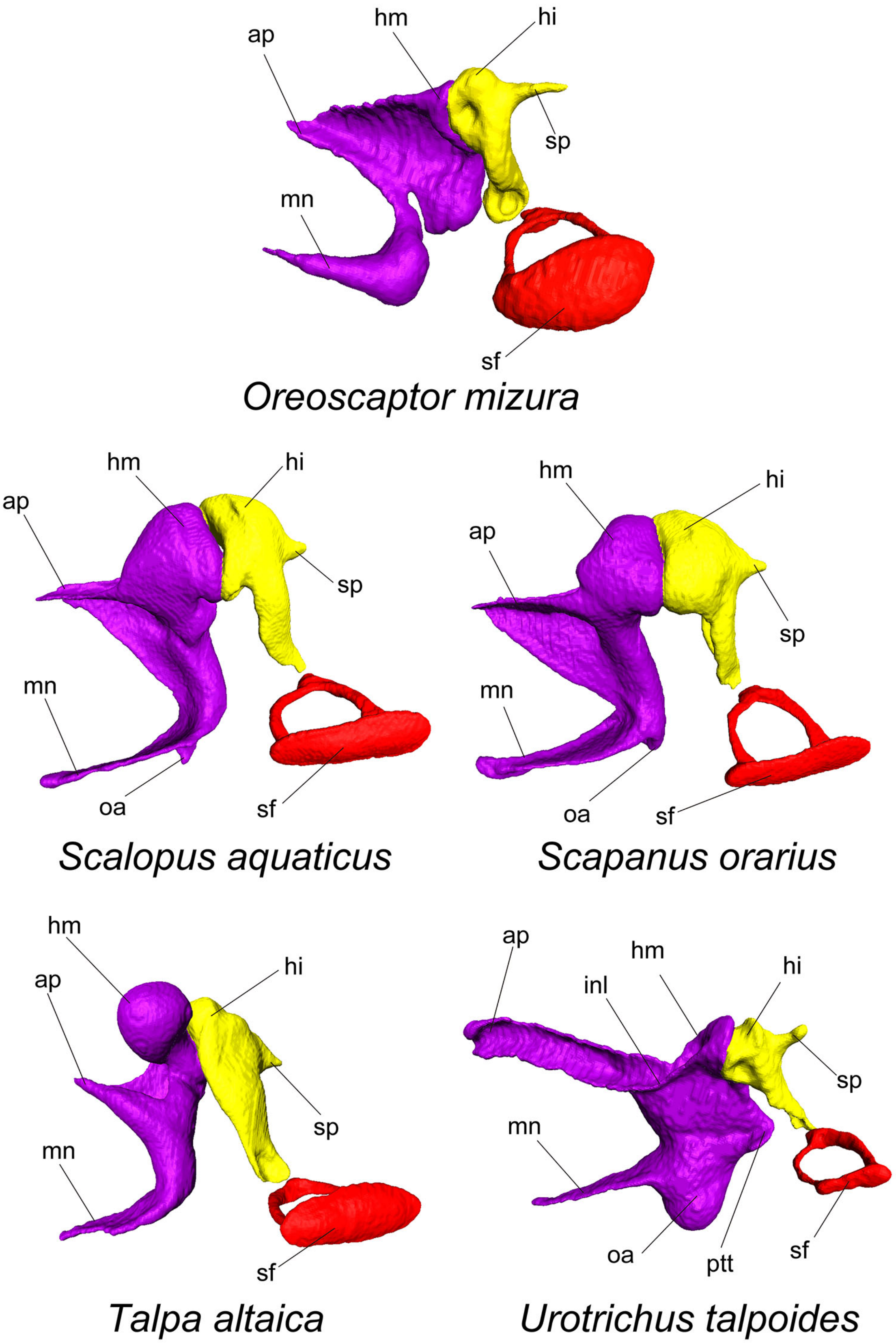
The anterior process of the malleus is not robust and and is similar in length with the manubrium (Fig.4). The anterior process and manubrium form a U-shaped curve as in other fossorial Eurasian talpids. The head of the malleus is globular as reported for *T. europaea*, *T. caeca*, and *T. romana* by Stroganov (1945). The cone-shaped body of the malleus has a large cavity, as reported in other *Talpa* (Stroganov, 1945). An orbicular apophysis of the malleus is completely absent. The articulation between the malleus and incus is loose. The short process of the incus is present but not large. Its incus is proportionally larger than other studied talpids. The stapes is also enlarged. The footplate of the stapes is flat and not rounded as in *Mogera*, *Euroscaptor*, and *Oreoscaptor*.

Urotrichus talpoides

This Japanese shrew mole is a semi-fossorial talpid which is not capable of digging deep tunnels (Ohdachi et al., 2009). The overall malleus shape differs from fully fossorial Eurasian talpids and fully fossorial American talpids, and is rather similar to soricids, erinaceids, and *N. gibbsii*, another semi-fossorial talpid in North America. The anterior process of the malleus is robust and longer than the manubrium (Fig.4). The anterior process and manubrium are nearly parallel and do not form a U-shaped curve. An orbicular apophysis of the malleus is absent as in soricids, erinaceids, and *N. gibbsii*. The stapes and incus are proportionally smaller than the malleus, which is in contrast to fully fossorial talpids. The footplate of the stapes is thin and flat.

Phylogenetic and ecological patterns of the middle ear ossicles

Table 2 summarizes the ossicular features of each taxon of the study. Among our sampled species, I observed that the footplate morphology is inflated and convex externally in *M. wogura*, *E. klossi*, *E. malayana*, *O. mizura*, all of which are



Oreoscaptor mizura

Scalopus aquaticus

Scapanus orarius

Talpa altaica

Urotrichus talpoides

Figure 4. Three-dimensional models of the middle ear ossicles of Talpidae (*Oreoscaptor mizura*, *Scalopus aquaticus*, *Scapanus orarius*, *Talpa altaica*, and *Urotrichus talpoides*).

East Eurasian members of Talpini (see also Sánchez-Villagra et al., 2006). *Tapla europaea* (Mason, 2006), *T. romana* (Stroganov, 1945), and *T. altaica* do not show this inflation in the stapes. It is now clear from molecular evidence that the *Mogera*, *Euroscaptor*, and *Oreoscaptor* form a sister group to *Talpa* (Fig.1; Shinohara et al., 2014). Given these, it is possible that this inflated footplate is a derived trait among East Eurasian members of Talpini. In theory, inflated footplate should increase the footplate area ratio against the tympanic membrane, resulting in reduction of impedance transformation performance (Burda et al., 1992). Reduction of impedance transformation performance is suggested as a typical pattern for highly subterranean animals which depend heavily on low-frequency sounds (Burda et al., 1992). However, both *Talpa* and *Mogera* are accepted as highly fossorial groups (Godfrey, 1955; Yokohata, 2005; Ohdachi et al., 2009), and it is counterintuitive to assume that *Mogera* is further specialized in fossorial lifestyle than *Talpa*. In this regard, it is worth noting that the incus is massively enlarged in *Talpa* compared to *Mogera*, *Euroscaptor*, and *Oreoscaptor*. This suggests that the ratio of incus lever arm against malleus lever arm is increased in *Talpa*. The increase of lever ratio will result in reduction of impedance transformation performance (Burda et al., 1992). Thus, reduction of impedance transformation performance is achieved by an enlarged footplate in East Eurasian Talpini whereas it is achieved by an enlarged incus in West Eurasian Talpini. This suggests that specialization for low-frequency sounds in the middle ear ossicles could have occurred independently in these two linages. Independent evolution of fossorial specialization has been widely accepted for American Talpini and Eurasian Talpini, and some authors argue such specialization could have occurred more than twice (see also Yates and Moore, 1990; Whidden, 2000; Shinohara et al., 2003; Motokawa, 2004). In this regard, differing pathways in reducing impedance transformation performance found in East Eurasian Talpini and West Eurasian Talpini may be of interest for future studies on subterranean convergence in talpids.

The short process of the incus is well developed in talpids, whereas it is less developed in erinaceids and soricids. Protrusion of the short process in *O. mizura* is remarkable among the studied eulipotyphlans. The shape of the malleus head is globular in *T. altaica*. This globular head is similarly found in *T. europaea*, *T. caeca*, and *T. romana* (Stroganov, 1945), a feature which seems to be found only in *Talpa*. *Talpa* is also unique in that they have an open cavity on the malleus. *Scapanus townsendii* (Mason, 2006), *Scapanus orarius*, and *Scalopus aquaticus*, those which belong to Scalopini, are characterized by proportionally enlarged malleus head and enlarged incus head. In contrast to Scalopini and West Eurasian Talpini, the malleus head is relatively small in East Eurasian Talpini. The overall middle ear morphology is conservative within East Eurasian Talpini, except that *Mogera* has a slender manubrium compared to *Euroscaptor* and *Oreoscaptor*.

Among the reported species, *C. platycephala* and *C. cristata* are semi-aquatic forms. However, convergence in morphology was hardly identified for these two. Aquatic pattern is unclear from the comparison here, thus comparisons with desmans (*Desmana moschata*, *Galemys pyrenaicus*) and water shrews (*Neomys fodiens*, *Sorex palustris*) are awaited. On the other hand, convergence appears to be evident for subterranean lifestyle. The inner lamina of the malleus is present in erinaceids, soricids, and less fossorial talpids (*C. cristata*, *N. gibbsii*, and *U. talpoides*) while it is absent in highly fossorial moles (*E. klossi*, *E. malayana*, *O. mizura*, *M. wogura*, *Scalops*, *Scapanus*, and *T. altaica*). Similarly, the orbicular apophysis is found in erinaceids, soricids, and less fossorial talpids whereas it is absent or rudimentary in highly fossorial moles. The anterior process and manubrium are slender and long in erinaceids, soricids, and less fossorial talpids. The articular surface between the malleus and incus appears to be larger in highly fossorial talpids. The muscular process for tensor tympani is not well developed in highly subterranean talpids. In contrast, it is evident in terrestrial and semi-subterranean eulipotyphlans. In agreement with previous reports (Burda et al., 1992; Mason, 2001), the stapes footplate is expanded in highly fossorial talpids, and smaller in less fossorial talpids and in terrestrial eulipotyphlans.

CONCLUSION

To date, comparative studies on the middle ear ossicles were very little reproducible due to the lack of open-access data. I provided a 3D atlas of three families over four and briefly described the middle ear ossicles of Erinaceidae (one species), Talpidae (ten species) and Soricidae (four species). Recently resolved phylogeny of this group and the comparative atlas presented here should shed light on how morphological traits of the middle ear ossicles may have evolved with functional specialization. The provided surfaces will encourage investigations especially by geometric morphometric analyses and biomechanical approaches.

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Family	Species	Length of ap	Pres./abs. of oa	Protrusion of sp	Shape of sf
Erinaceidae	*Erinaceus europaeus*	longer than mn	present	round-shaped	flat
Soricidae	*Anourosorex yamashinai*	longer than mn	present	not evident	flat
	Blarina brevicauda	slightly longer than mn	present	not evident	flat
	Chimarrogale platycephala	slightly longer than mn	present	not evident	flat
	Suncus murinus	comparable to mn	present	round-shaped	flat
Talpidae	*Condylura cristata*	shorter than mn	present	evident	flat
	Euroscaptor klossi	comparable to mn	absent	evident	inflated
	Euroscaptor malayana	comparable to mn	absent	evident	inflated
	Mogera wogura	comparable to mn	absent	evident	inflated
	Neurotrichus gibbsii	longer than mn	present	evident	flat
	Oreoscaptor mizura	shorter than mn	absent	evident	inflated
	Scalopus aquaticus	comparable to mn	slightly present	evident	flat
	Scapanus orarius	comparable to mn	slightly present	evident	flat
	Talpa altaica	comparable to mn	absent	evident	flat
	Urotrichus talpoides	longer than mn	present	evident	flat

Table 2. Summary of the ossicular features of studied animals. Abbreviations: ap, anterior process of malleus; mn, manubrium; oa, orbicular apophysis; sf, footplate of stapes; sp, short process of incus.

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