

New Dental Anomalies in the Greater Japanese Shrew Mole Urotrichus talpoides (Eulipotyphla: Talpidae)

Authors: Okabe, Shinya, Shinohara, Akio, and Motokawa, Masaharu

Source: Mammal Study, 46(4) : 309-315

Published By: Mammal Society of Japan

URL: https://doi.org/10.3106/ms2020-0095

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

New dental anomalies in the greater Japanese shrew mole *Urotrichus talpoides* (Eulipotyphla: Talpidae)

Shinya Okabe^{1,2,*}, Akio Shinohara³ and Masaharu Motokawa⁴

¹ Graduate School of Science, Kyoto University, Kitashirakawa-Oiwakecho, Sakyo, Kyoto 606-8502, Japan

² Research Fellow of Japan Society for the Promotion of Science

³ Division of Bio-resources, Department of Biotechnology, Frontier Science Research Center, University of Miyazaki, Kihara

5200, Kiyotake, Miyazaki 889-1692, Japan

⁴ The Kyoto University Museum, Kyoto University, Sakyo, Kyoto 606-8501, Japan

Abstract. Dental anomalies in the greater Japanese shrew mole *Urotrichus talpoides* Temminck, 1841 (Eulipotyphla: Talpidae) were examined, based on 1001 specimens. We followed the dental formula of *U. talpoides* I 2/1, C 1/1, P 4/3, M 3/3 = 36, which is adopted by the most recent Japanese researchers, and found dental anomalies in 17 specimens involving 12 instances of absent tooth, four of extra tooth, and one of connate tooth. Of these, the following dental anomalies are reported in *U. talpoides* for the first time: extra tooth posterior to the upper canine (C¹), extra tooth posterior to the upper second premolar (P²), extra teeth on the inner sides of the upper fourth premolars (P⁴), and connate tooth on the lower canine (C₁). The most frequently observed dental anomaly was the absent tooth on C¹ (52.9%), whereas the others were not common (< 11.8%). Our results indicate that dental anomalies in *U. talpoides* in Urotrichini possess the different pattern from those in species in Scalopini and Talpini. On the other hand, alternative hypothesis of dental formula I 3/2, C 1/1, P 3/2, M 3/3 = 36 explains the observed anomaly pattern in line with the general trend of dental anomalies in Talpini and Scalopini.

Key words: absent tooth, connate tooth, dental formula, extra tooth, Urotrichini.

Dental anomalies have been known at low frequencies in representative species for most orders of mammals (Feldhamer et al. 2020) but reported as an exceptionally high occurrence in a few species of subfamily Talpinae, family Talpidae, order Eulipotyphla (Stein 1962; Kawada et al. 2006, 2011). Talpinae is therefore an interesting subfamily to study dental anomalies. The size and shape of each tooth have been differentiated among five tribes of Talpinae, reflecting the evolutionary process (Motokawa 2004). Dental characteristics of those five tribes in reference to the incisors and canines are as follows: in Talpini (Euroscaptor, Mogera, Oreoscaptor, Parascaptor, Scaptochirus, and Talpa), the incisors are small, but the upper canine (C¹) is significantly large; in Condylurini (Condylura), the upper second incisor (I^2) is larger than the upper first incisor (I¹), which exceeds the size of C¹; in Desmanini (Desmana and Galemys), I¹ is heavily

large, while I², the upper third incisor (I³), and C¹ are small; in Scalopini (*Scalopus*, *Scapanus*, *Parascalops*, and *Scapanulus*), I¹ is large and larger than C¹, and I² and I³ are small; in subtribe Urotrichina of Urotrichini (*Dymecodon*, *Neurotrichus*, and *Urotrichus*), I¹ is large, I² is secondarily large, and C¹ is small; and in subtribe Scaptonychina of Urotrichini (*Scaptonyx*), I¹ is smaller than C¹ (Abe 2007; Kryštufek and Motokawa 2018).

In Talpini, Scalopini, and Urotrichini, dental anomalies have been reported, such as extra, absent, or connate teeth: 14 species in Talpini, four species in Scalopini, and two species in Urotrichini (Hall 1940; Miyao 1972; Imaizumi and Kubota 1978; Hoffmann 1984; Kawada et al. 2006; Feldhamer and Towery 2011; Kawada et al. 2011; Asahara et al. 2012; Sasaki 2016; Kryštufek and Motokawa 2018). An extra tooth is defined as an additional tooth with normal dentition possessing a crown

^{*}To whom correspondence should be addressed. E-mail: okabe.shinya.57a@st.kyoto-u.ac.jp

with independent root as seen in surface observations; an absent tooth is defined as congenital and postnatal tooth loss, excluding tooth loss after birth with roots or alveoli remaining as seen in surface observations; and a connate tooth is two teeth sharing the same root (Miles and Grigson 1990; Kawada et al. 2006, 2011). In Condylurini, no dental anomalies were found in 14 specimens of *Condylura cristata*. In Desmanini, there has been no report regarding dental anomalies.

In Talpini, dental anomalies have been found primarily for premolars (97.1% of all dental anomalies as found in 739 examples), comprising absent (76.9%), connate (13.5%), and extra premolars (6.7%) (Kryštufek et al. 2001; Kawada et al. 2006, 2011; Asahara et al. 2012). In Scalopini, dental anomalies include absent premolars (73.8%) and absent incisors (24.6%) (Hall 1940; Feldhamer and Towery 2011). In Urotrichini, dental anomalies were reported in *Urotrichus talpoides*, as absent canines (7.7% in 246 individuals) and premolars (10.5%) (Miyao 1972), an extra tooth between C₁ and the lower second premolar (P₂) (0.36% in 1120 individuals) (Imaizumi and Kubota 1978; Sasaki 2016), and extra tooth in premolars (0.8% in 246 individuals) (Miyao 1972), as well as in *Dymecodon pilirostris* as absent canines and premolars (Miyao 1972).

These dental anomalies in Talpinae have been mostly reported for incisors or premolars, while fewer examples have been known for canines or molars (Hall 1940; Hoffmann 1984; Kawada et al. 2006, 2011; Feldhamer and Towery 2011; Asahara et al. 2012). Canine dental anomalies in Talpinae have been reported only in four species—one case of extra upper canine in Mogera wogura (Kawada et al. 2011), one case of an absent upper canine in Scapanus latimanus (Hall 1940), 17 cases of absent upper canine and two cases of absent lower canine in U. talpoides (Miyao 1972), and two cases of absent upper canine in D. pilirostris (Miyao 1972). In terms of molar dental anomalies, ten cases of an extra tooth distal to the third upper molar and an extra tooth distal to the third lower molar have been reported only in Talpa altaica (Kawada et al. 2006).

Urotrichus talpoides in Urotrichini is an interesting species within Talpinae involving high occurrence of absent canine among 246 specimens (Miyao 1972). On the other hand, no case of dental anomaly in canine has been found in the following studies that examined 1120 specimens of the species (Imaizumi and Kubota 1978; Sasaki 2016).

Herein, the frequent occurrence of C^1 dental anomaly is the characteristics of the dental anomaly of *U. talpoides*. In addition, it should be noted that the position of C^1 is different between two different hypotheses of dental formula for U. talpoides: I 2/1, C 1/1, P 4/3, M 3/3 = 36including ante-molars I^1 , I^2 , C^1 , P^1 , P^2 , P^3 , P^4/I_2 , C_1 , P_2 , P_3 , P₄, was proposed by Imaizumi and Kubota (1978); while I 3/2, C 1/1, P 3/2, M 3/3 = 36 including ante-molars I^1 , I^2 , I^3 , C^1 , P^1 , P^3 , P^4 / I_2 , I_3 , P_1 , P_3 , P_4 , was proposed by Ziegler (1971). Imaizumi and Kubota (1978) regarded the fifth tooth before M^1 as C^1 , based on the definition that C^1 appears at sutura incisiva; while fourth tooth before M¹ is C^1 following Ziegler (1971). Though the dental formula of Imaizumi and Kubota (1978) has been widely accepted, Kawada et al. (2001) reconsidered the tooth formula of Desmana moschata and revealed that C1 position would not be detected by surface position of sutura incisiva and implied that I 3/2, C 1/1, P 3/2, M 3/3 = 36(same as Ziegler 1971) might be suitable for U. talpoides. Herein, we conducted a comprehensive study of dental anomalies in U. talpoides based on 1001 specimens and discussed their significance in reference to dental formulae within Talpinae.

Materials and methods

We examined 1001 skulls of adult *U. talpoides* collected from a wide range of its distribution in Honshu, Kyushu, Shikoku, Tsushima Island, and Oki Islands in Japan. Specimens are stored at the Botanical Garden, Field Science Center for Northern Biosphere of Hokkaido University, Sapporo (HUNHM); the Kyoto University Museum, Kyoto University, Kyoto (KUZ); the National Museum of Nature and Science, Tsukuba (NSMT); and the private collection of Akio Shinohara (SAS; HEG).

We followed the dental formula proposed by Imaizumi and Kubota (1978): (I¹, I², C¹, P¹, P², P³, P⁴, M¹, M², M³/ I₂, C₁, P₂, P₃, P₄, M₁, M₂, M₃ = 36). This dental formula was initially mentioned in a brief report of Imaizumi (1949) without a detailed description and had been referred to in later literatures (Imaizumi 1960; Imaizumi and Obara 1966). After the formal description of this dental formula by Imaizumi and Kubota (1978), it is well accepted until recently (Sasaki 2016). We conducted surface observations of the upper and lower dentitions (Fig. 1) under a microscope and identified three types of dental anomalies, i.e., the absent, extra, and connate teeth. We excluded obvious postnatal tooth loss, whereby teeth roots or alveoli remained on the surface of the jaws as observed following the procedure of Kawada et al. (2011).

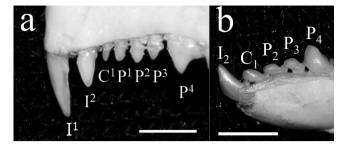


Fig. 1. Normal dentition of ante-molars in *Urotrichus talpoides* according to the dental formula proposed by Imaizumi and Kubota (1978). The upper first incisor (I^1) to the upper fourth premolar (P^4) (a; KUZ M7104), and the lower second incisor (I_2) to the lower fourth premolar (P_4) (b; KUZ M582). The scale bar represents 2 mm.

Results

Seventeen cases (1.7%) of dental anomalies were found in 1001 specimens examined. A single kind of anomaly was found in each individual with a dental anomaly. Of these, 12 specimens (70.6% of all anomalous specimens) had the absent tooth, four specimens (23.5%) had the extra tooth, and one specimen (5.9%) had the connate tooth (Table 1). These dental anomalies were associated with the canines or premolars in the upper and lower dentitions.

The absent tooth of C¹ was found in nine specimens (NSMT M19695, NSMT M7561, NSMT M23436, KUZ M7145, KUZ M7146 [Fig. 2a], HUNHM 53084, HUNHM 52572, HUNHM 53118, and HUNHM 50716)-presented bilaterally in six specimens and unilaterally in three specimens. The absent tooth of P¹ was detected in two specimens (HUNHM 53130 [Fig. 2b], HUNHM 50717)presented unilaterally in both specimens. The absent tooth of P² was found in one specimen (HUNHM 50715 [Fig. 2c])—presented bilaterally (Fig. 2). Rearrangement of the positions of the teeth was observed in the cases involving the absent tooth. In cases of absent C¹ dentition, the small teeth posterior to C1 (P1, P2, and P3) were located moderately anterior to make the space corresponding to the absent tooth smaller; in cases of absent P¹ dentition, C¹ was located posteriorly and P² was transferred anteriorly; and in a case of absent P², P¹ was located posteriorly.

Unilateral extra tooth posterior either to C^1 or to P^2 was found in one specimen each (NSMT M5319 [Fig. 3a] and KUZ M7282 [Fig. 3b], respectively). Extra teeth were also found on the inner side of P^4 in one specimen (HUNHM 52235 [Fig. 3c]) and presented bilaterally. Another extra tooth on the lower jaw was found posterior to C_1 in one specimen (KUZ M748 [Fig. 3d]) and

Table 1. Number of specimens with absent, extra, and connate teeth observed in Urotrichus talpoides

		Anomaly tooth										
Dental anomaly <i>n</i>		C^1	\mathbb{P}^1	\mathbb{P}^2	\mathbb{P}^4	C_1						
Absent teeth	12	9 (6 bilateral, 1 right, 2 left)	2 (2 left)	1 (1 bilateral)	_	_						
Extra teeth	4	1 (1 right)	_	1 (1 left)	1 (1 bilateral)	1 (1 left)						
Connation	1	_	_	_	_	1 (1 left)						
Total	17	10	2	2	1	2						

 C^1 : the upper canine, P^1 : the upper first premolar, P^2 : the upper second premolar, P^4 : the upper fourth premolar, and C_1 : the lower canine

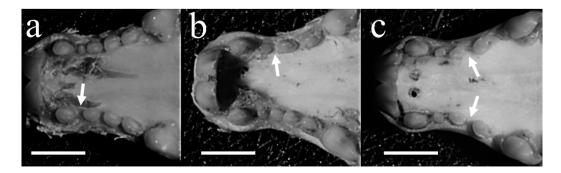


Fig. 2. Three cases of absent teeth (arrows) in *Urotrichus talpoides*. Absent tooth of the upper canine (C^1) on the right side (a; KUZ M7146), absent tooth of the upper first premolar (P^1) on the left side (b; HUNHM 53130), absent teeth of the upper second premolar (P^2) on the right and left sides (c; HUNHM 50715). The scale bar represents 2 mm.

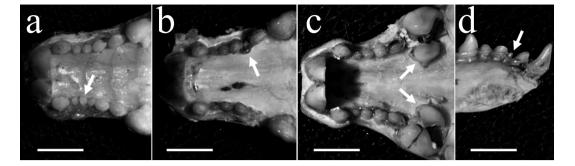


Fig. 3. Four cases of extra teeth (arrows) in *Urotrichus talpoides*. An extra tooth posterior to the upper canine (C^1) on the right side (a; NSMT M5319), an extra tooth posterior to the upper second premolar (P^2) on the left side (b; KUZ M7282), extra teeth on the lingual side of the upper fourth premolar (P^4) on the right and left sides (c; HUNHM 52235), and an extra tooth posterior to the lower canine (C_1) on the left side (d; KUZ M748). The scale bar represents 2 mm.

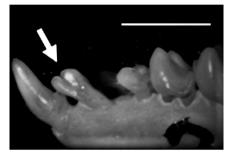


Fig. 4. A case of a connate tooth (arrow) on the lower canine (C_1) in left side in *Urotrichus talpoides* (NSMT M26663). The space posterior to the connate tooth was caused by a broken premolar tooth. The scale bar represents 2 mm.

presented unilaterally (Fig. 3). These extra teeth located posterior to C^1 , P^2 , or C_1 were slender teeth with a tiny single cusp, whereas the extra teeth located on the inner side of P^4 had a well-developed triangular crown with the length two-thirds of P^4 (Fig. 3c).

A connate tooth on C_1 was found in one specimen (NSMT M26663) and presented unilaterally (Fig. 4). Although the normal C_1 is a small unicuspid tooth (Fig. 1), the connate C_1 had a slightly bulging and two-lobed crown, sharing the same neck and root of the tooth (Fig. 4).

Discussion

The frequency of all dental anomalies in *U. talpoides* was 1.7% based on 1001 specimens in the present study, and it is low among talpine species: Talpini, 22.9% in *T. altaica* (n = 1789), 17.5% in *M. tokudae* (n = 57), 9.9% in *M. robusta* (n = 241), 6.4% in *M. wogura* (n = 687), 1.8% in *M. imaizumii* (n = 331) (Kawada et al. 2006, 2011; Asahara et al. 2012); Scalopini, 14.5% in *Scalopus aquaticus* (n = 249), 8.7% in *S. latimanus* (n = 265), and

1.2% in *S. orarius* (n = 81) (Hall 1940; Feldhamer and Towery 2011); Urotrichini, 20.4% in *D. pilirostris* (n =54) (Miyao 1972). Such lower occurrence of the dental anomaly in *U. talpoides* coincides with 0.36% in the previous studies (n = 1120; Imaizumi and Kubota 1978; Sasaki 2016). In contrast, the higher frequency (15.0%) in *U. talpoides* (n = 246) was reported by Miyao (1972). The reason responsible for such differences is uncertain.

In the present study, three kinds of dental anomalies were detected at four different tooth positions in *U. talpoides*. Extra teeth posterior to C^1 , posterior to P^2 , or posterior to P^4 (Fig. 3) and a connate tooth on C_1 (Fig. 4) were reported for the first time. The remaining dental anomalies of a small single cusped extra tooth posterior to C_1 (Imaizumi and Kubota 1978; Sasaki 2016) and absent C^1 , P^1 , P^2 (Miyao 1972) have been reported previously.

All the absent teeth in *U. talpoides* represented the small teeth, C^1 , P^1 , and P^2 . For these small haplodont teeth of *U. talpoides*, the conical C^1 is slightly smaller than the cone-shaped P^1 , and teeth sizes increase to be $C^1 < P^1 < P^2$ (Fig. 1). In contrast to teeth size, the frequency of absent teeth was observed as $C^1 > P^1 > P^2$ (Table 1), which indicates that smaller teeth are more likely to be absent.

The extra tooth posterior to C^1 and the extra tooth posterior to C_1 were small conical teeth. The extra tooth posterior to C_1 was considered as a result of atavistic event of the lower first premolar (P₁) which had been lost in the evolutionary process of Urotrichini (Imaizumi and Kubota 1978; Sasaki 2016). However, it is difficult to conceive that the tooth reverted to P₁ according to the law of irreversibility (Gould 1970). The morphology of the extra tooth was too diminutive and thin to be recognized as P₁. The extra tooth posterior to P² was chisel-shaped (Fig. 5), similar to the extra premolars in *T. altaica* and *M. robusta* in Talpini (Kawada et al. 2006; Asahara et al.



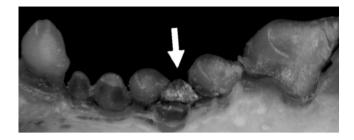


Fig. 5. A chisel-shaped extra tooth between P^2 and P^3 in left side in *Urotrichus talpoides* (KUZ M7282).

2012). The extra tooth located at the inner position of P⁴ had a unique morphology—a well-developed triangular crown—but was slightly smaller than P⁴. The deciduous P⁴ of *U. talpoides* also has a well-developed triangular crown and is smaller than a permanent P⁴ (personal observation), similar to this extra P⁴. This extra P⁴ might be a persistent deciduous tooth, similar example to the extra tooth on the buccal side of P⁴ in *T. altaica* in Talpini (Kawada et al. 2006).

The connate tooth has been reported in mandibular premolars in *T. altaica* and *M. wogura* in Talpini (Kawada et al. 2006, 2011). However, the connate tooth of *U. talpoides* in the present study was C_1 , and this is the first report of a connate C_1 in Talpinae.

The dental anomalies in *U. talpoides* involved canine and premolars but did not involve incisors. Dental anomalies in Talpinae have been reported to involve incisors, canine, and premolars (Hall 1940; Hoffmann 1984; Kryštufek et al. 2001; Kawada et al. 2006; Feldhamer and Towery 2011; Kawada et al. 2011; the present study). Interestingly, dental anomalies occur in the incisor row in both Scalopini and Talpini, but not in Urotrichini. Canine dental anomalies are few in Talpini and Scalopini, and only an example of extra canine in *M. wogura* (Kawada et al. 2011) in Talpini and an absent canine in *S. latimanus* (Hall 1940) in Scalopini have been reported. Canine anomalies in Urotrichini, on the contrary, involve extra, absent, and connate teeth in the upper and lower dentitions of *U. talpoides* in the present study.

Such differences in canine anomalies between *U. talpoides* and species in Scalopini or Talpini may be related to the size and arrangement of the teeth: *U. talpoides* has short, thin, weak, and small canine (Fig. 1) (Imaizumi and Kubota 1978), whereas Scalopini and Talpini have large canine (Kryštufek and Motokawa 2018). As dental anomalies usually involve small teeth with less functionality (Hall 1940), the small and less functional canine of *U. talpoides* may be subject to frequent dental anomalies.

Two different dental formulae should also be reconsidered for *U. talpoides* to understand the differences between Urotrichini and Scalopini / Talpini. We followed the formula I 2/1, C 1/1, P 4/3, M 3/3 = 36, which includes ante-molars as follows: I¹, I², C¹, P¹, P², P³, P⁴/I₂, C₁, P₂, P₃, P₄, with a diphyodont P¹ and a monophyodont P², based on the sutura incisiva as an indicator of the canine position (Imaizumi and Kubota 1978). In contrast, another dental formula I 3/2, C 1/1, P 3/2, M 3/3 = 36, which includes ante-molars as follows: I¹, I², I³, C¹, P¹, P³, P⁴ / I₂, I₃, P₁, P₃, P₄, with a monophyodont P¹, was described by Ziegler (1971) based on the first premolar position.

The most common dental anomaly involved C^1 in the present study following the dental formula of Imaizumi and Kubota (1978), but this tooth could be alternatively regarded as I³ when adopting the dental formula of Ziegler (1971). Indeed, it is unclear whether observations of the sutura incisiva only from the cranium surface is a reliable indicator of the canine position, as Kawada et al. (2001) revealed that the position of sutura incisiva was inconsistent with the position of the canine in *D. moschata* in Desmanini. Furthermore, following the dental formula of Imaizumi and Kubota (1978), *U. talpoides* should be an exceptional species among living placentals that possesses a diphyodont P¹.

Here, the most frequently observed dental anomaly of U. talpoides involved I^3 if we adopt the alternative dental formula of Ziegler (1971). Accordingly, the high occurrence of I³ dental anomalies is shared among Urotrichini, Scalopini, and Talpini, while frequency of a canine dental anomaly turns to be low-two absent C1 in U. talpoides in Urotrichini (Table 2) as well as an extra canine in M. wogura in Talpini (Kawada et al. 2011) and an absent canine in S. latimanus in Scalopini (Hall 1940). The most frequent dental anomaly at the I³ position in U. talpoides may be explained by the terminal reduction and addition theory (Koyasu 1993), which hypothesized that tooth reduction or addition occurred in the anterior or posterior regions of incisors, premolars, or molars. As well, it is convincing that "a diphyodont P1" in U. talpoides corresponds to a diphyodont C¹, and P¹ become monophyodont as in Scalopini, Talpini and most placentals (Hall 1940; Hoffmann 1984; Kawada et al. 2006; Feldhamer and Towery 2011; Kawada et al. 2011; Asahara et al. 2012). Our results suggested that more stable and appropriate dental formula would be that proposed by Ziegler (1971), and we recommend adopting this dental formula for U. talpoides.

 Table 2.
 Comparison of number of dental anomalies at each dental position in ante-molars of Urotrichus talpoides in following two different dental formulae of Imaizumi and Kubota (1978) and Ziegler (1971)

	Dental anomalies															
Dental formula	Upper dentition							Lower dentition								
-	\mathbf{I}^1	I^2	I^3	C^1	\mathbf{P}^1	\mathbf{P}^2	\mathbf{P}^3	\mathbf{P}^4	I_1	I_2	I_3	C_1	\mathbf{P}_1	P_2	P ₃	P ₄
Imaizumi and Kubota (1978)	0	0	_	10	2	2	0	1	_	0	_	2	_	0	0	0
Ziegler (1971)	0	0	10	2	2	_	0	1	_	0	2	_	0	_	0	0

Acknowledgments: We are grateful to Kato, M., Takaya, H., and the staff of the Botanical Garden, Field Science Center for Northern Biosphere, Hokkaido University, Japan; Kawada, S. and the staff of the National Museum of Nature and Science, Japan, for allowing us to examine specimens under their care. The present study was supported by a JSPS KAKENHI grant (JP18H03602).

References

- Abe, H. 2007. Illustrated Skulls of Japanese Mammals. Hokkaido University Press, Sapporo, 290 pp. (in Japanese).
- Asahara, M., Kryukov, A. and Motokawa, M. 2012. Dental anomalies in the Japanese mole *Mogera wogura* from northeast China and Primorsky region of Russia. Acta Theriologica 57: 41–48.
- Feldhamer, A. G., Merritt, F. J., Krajewski, C., Rachlow, L. J. and Stewart, M. K. 2020. Mammalogy, Fifth edition. Johns Hopkins University Press, Baltimore, 725 pp.
- Feldhamer, A. G. and Towery, N. B. 2011. Dental anomalies in the Eastern Mole (*Scalopus aquaticus*). The American Midland Naturalist 165: 421–425.
- Gould, J. S. 1970. Dollo on Dollo's law: irreversibility and the status of evolutionary laws. Journal of the History of Biology 3: 189–212.
- Hall, E. R. 1940. Supernumerary and missing teeth in wild mammals of the orders Insectivora and Carnivora, with some notes on disease. Journal of Dental Research 19: 103–143.
- Hoffmann, R. S. 1984. A review of the shrew-moles (genus *Uropsilus*) of China and Burma. Journal of the Mammalogical Society of Japan 10: 69–80.
- Imaizumi, Y. 1949. The Natural History of Japanese Mammals. Yoyoshobo, Tokyo, 348 pp. (in Japanese).
- Imaizumi, Y. 1960. Colored Illustrations of the Mammals of Japan. Hoikusha, Osaka, 196 pp. (in Japanese).
- Imaizumi, Y. and Obara, H. 1966. A Natural History of Mammals of the World Insectivora & Dermoptera. Shin-shichyo-sha, Tokyo, 365 pp. (in Japanese).
- Imaizumi, Y. H. and Kubota, K. 1978. Numerical identification of teeth in Japanese shrew-mole, *Urotrichus talpoides* and *Dymecodon pilirostris*. Journal of Tokyo Medical and Dental University 25: 91–99.
- Kawada, S., Endo, H., Oda, S. and Koyasu, K. 2011. Dental anomalies in four mole species of the genus *Mogera* (Insectivora, Talpidae)

from Japan. Journal of National Museum of Nature and Science 37: 63–72.

- Kawada, S., Koyasu, K., Zholnerovskaya, I. E. and Oda, S. 2001. Reconsideration of the tooth formula of *Desmana moschata* and problem in the processes of it's decision. Journal of Special Publication of Nagoya Society of Mammalogists 3: 41–48 (in Japanese).
- Kawada, S., Koyasu, K., Zholnerovskaya, I. E. and Oda, S. 2006. Analysis of dental anomalies in the Siberian mole, *Talpa altaica* (Insectivora, Talpidae). Journal of Archives of Oral Biology 51: 1029–1039.
- Koyasu, K. 1993. Variability of dentition in the bat-eared fox, *Otocyon megalotis*. The Aichi-Gakuin Journal of Dental Science 31: 63–104 (in Japanese with English summary).
- Kryštufek, B. and Motokawa, M. 2018. Family Talpidae (moles, desmans, star-nosed moles and shrew moles). In (Wilson, E. D. and Mittermeier, A. R., eds.) Handbook of the Mammals of the World, Vol. 8 Insectivores, Sloths and Colugos, pp. 552–619. Lynx editions, Barcelona.
- Kryštufek, B., Spitzenberger, F. and Kefelioglu, H. 2001. Description, taxonomy, and distribution of *Talpa davidiana*. Mammalian Biology 66: 135–143.
- Miles, A. E. W. and Grigson, C. 1990. Colyer's Variations and Diseases of the Teeth of Animals, Revised edition. Cambridge University Press, Cambridge, 672 pp.
- Miyao, T. 1972. Supernumerary and missing teeth in four species of the order Insectivora. Journal of Growth 11: 21–27 (in Japanese with English abstract).
- Motokawa, M. 2004. Phylogenetic relationships within the family Talpidae (Mammalia: Insectivora). Journal of Zoology 263: 147– 157.
- Sasaki, A. 2016. One pair of supernumerary lower first premolar of the Japanese shrew-mole *Urotrichus talpoides*. Journal of Natural History of the Tokai District 9: 31–36.
- Stein, G. H. W. 1962. Anomalien der Zahnzahl und ihre geographische Variabilität bei Insectivoren: I. Maulwurf, *Talpa europaea* L. Mitteilungen aus dem Zoologischen Museum in Berlin 39: 223– 240 (in German).
- Ziegler, C. A. 1971. Dental homologies and possible relationships of recent Talpidae. Journal of Mammalogy 52: 50–68.

Received 25 September 2020. Accepted 26 April 2021. Published online 26 August 2021. Editor was Mugino Kubo.

Appendix 1.

List of the specimens examined in the present study, which have been stored in Botanic Garden, Field Science Center for Northern Biosphere in Hokkaido University, Sapporo (HUNHM); The Kyoto University Museum, Kyoto University, Kyoto (KUZ); National Museum of Nature and Science, Tsukuba (NSMT); and private collection of Akio Shinohara (SAS; HEG).

HUNHM 50715-50179, 50885, 50886, 50888-50891, 50895, 52084, 52085, 52095, 52226-52239, 52556-52567, 52569-52575, 52577, 52578, 52588, 52589, 52591, 52593-52595, 52597-52615, 52620, 52624, 52625, 52627, 52628, 52630-52637, 52639, 52640, 52643-52649, 52654-52657, 52659-52661, 52665, 52666, 52670, 52673-52678, 52681, 52682, 52685-52700, 53056-53059, 53061-53141, 53143-53153, 53155-53164, 53321-53324, 53327-53332, 53335-53338, 55257, 55793, 55794, 55897-55902, 55904-55906, 55945, 55946, 56070, 56093, 56119, 56175, 57688-57690, 57738, 57794-57844, 58362, 58363.

KUZ M071, M072, M117, M155, M200, M216, M217, M227, M236–M238, M288, M297–M309, M324, M336, M466–M468, M582, M583, M588, M590, M631, M634, M671, M709, M711, M716, M717, M726, M727, M729, M732, M733, M736–M739, M745, M747–M750, M838, M1021, M1289, M1302, M1329, M1507, M4430, M7099–M7106, M7111, M7113–M7137, M7139–M7174, M7176–M7200, M7202–M7210, M7212, M7213, M7215–M7223, M7225–M7230, M7232–M7250, M7252–M7284, M7286–M7298, M7300–M7305.

NSMT M1413, M1430, M1468, M1469, M1726, M2334, M2411, M2412, M2420, M2735, M2741, M2742, M2753, M2850, M2851, M2879, M2974, M2976, M2993, M2995, M3149–M3153, M3261, M3304, M3305, M3345, M3347, M3348, M3370, M3391, M3400, M3421, M3424– M3426, M3499, M3600, M3602, M3651, M3657, M3757, M3830–M3835, M3837, M3838, M3851–M3856, M3873, M3874, M3947, M3948, M4001, M4002, M4270, M4271, M4290, M4291, M4324, M4474, M4477, M4530–M4533, M4535b, M4537, M4541, M4542, M4577, M4578, M4673, M4674, M4748, M4928, M4929, M4943–M4945, M5070, M5071, M5091, M5113, M5128, M5154–M5156, M5204, M5205, M5314, M5316, M5319, M5326, M5327b, M5402–M5405, M5805, M6475, M7561, M7781, M7833, M8796–M8798, M8901, M8902, M8923, M8924, M8966, M8987, M9095, M9110, M9112, M9213, M9433, M9528, M9589, M9630, M9633, M9635, M9637, M9658, M9790, M9795–M9797, M9799, M9800, M9807, M9812–M9819, M9822, M9823, M9825, M9834, M9895, M9896, M9901, M9902, M9910, M10022, M10402, M10404, M10441, M10442, M10483, M10484, M10499-M10501, M10630, M11235, M11238, M11248, M11249, M11503, M11504, M11552-M11554, M11571, M11572, M11574, M11582, M11826, M12240, M12606, M12734, M12738, M12763, M12764, M12767, M12768, M12770, M12786, M12788, M13718, M13800, M13918, M13920, M14513, M14514, M14516, M16039, M16177, M16872, M16905, M16910–M16912, M16916, M16919, M17013, M17070, M17334, M17335, M17337, M17509, M17545, M17577, M17578, M17649, M17651, M17652, M17675-M17680, M17695-M17699, M17772-M17778, M17940, M19693-M19696, M19969, M20123, M20125, M20560, M20561, M20690, M21201, M21436, M21437, M21440–M21447, M21449, M21451–M21458, M21461–M21467, M21570, M21571, M23420, M23421, M23424–M23430, M23432, M23434–M23436, M23438, M23440, M23441, M23443, M23444, M23448, M23450–M23452, M23454, M23456, M23458–M23460, M23464, M23466–M23470, M23500, M23587, M23588, M25710, M25712–M25715, M26661–M26663, M26827, M27189–M27193, M27330, M27334-M27337, M27471, M27886, M28201-M28204, M28206, M28207, M28684, M28685, M28745, M28746, M29115, M29117, M29443, M29455-M29457, M33927.

SAS 1, 25–28, 31–38, 40–42, 46, 65, 67, 70.

HEG 84-97, 85-97, 95-97, 127-98, 132-98, 231-98, 233-98, 234-98, 235-98, 236-98, 237-98, 238-98, 239-98, 241-98, 242-98, 243-98, 244-98, 245-98, 248-98, 249-98, 250-98, 252-98, 253-98, 255-98, 256-98, 257-98, 258-98, 259-98, 261-98, 262-98, 263-98, 264-98, 266-98, 267-98, 268-98, 270-98, 271-98, 272-98, 277-98, 278-98, 279-98, 282-98, 283-98, 284-98, 285-98, 287-98.