

DENTAL ANOMALIES IN VIETNAMESE MOLES (Mammalia, Talpidae): PATTERNS AND DEVELOPMENTAL IMPLICATIONS

Giang Trong Toan^{1,*}, Nguyen Truong Son^{2,*}, Shinya Okabe^{3,*},
Masaharu Motokawa^{4,*}, Bui Tuan Hai^{5,*}

¹Vietnam National University of Forestry, Xuan Mai, Ha Noi, Vietnam

²Institute of Biology, Vietnam Academy of Science and Technology,
18 Hoang Quoc Viet, Ha Noi, Vietnam

³National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki 305-0005, Japan

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

⁵VNU University of Science, 334 Nguyen Trai, Thanh Xuan, Ha Noi, Vietnam

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ABSTRACT

Dental anomalies were examined in 148 specimens representing seven mole species of the genera *Euroscaptor* and *Mogera*, collected across Vietnam, a region corresponding to the southern range margin for many mole species. Dental anomalies were identified in 15 individuals (10.14%), including cases of oligodonty (n = 11), abnormally shaped teeth (n = 3), and a connate tooth (n = 1). Premolar oligodonty, particularly the absence of P2 and P3, was the most frequently observed anomaly, occurring in 7.43% of all specimens. The incidence of dental anomalies in *Euroscaptor ngoclinhensis* (16.67%) was notably higher than rates reported for some central populations of other talpid species. To investigate the potential underlying causes of this elevated anomaly rate, we tested the hypothesis that it reflects increased developmental instability, an established consequence of genetic drift and reduced gene flow in peripheral populations. No significant association was found between the presence of dental anomalies and overall craniodental size. However, quantitative analysis of bilateral skull traits revealed that individuals exhibiting dental anomalies also showed significantly elevated levels of fluctuating asymmetry, a widely recognized marker of developmental instability. These findings are discussed in the broader context of population genetics and developmental biology. We propose that the high prevalence of premolar oligodonty may be driven by an increased frequency of deleterious variants affecting conserved odontogenetic pathways, potentially involving key regulatory genes such as *MSX1* and *PAX9*. The Vietnamese mole populations provide a valuable model for exploring the relationship between developmental instability and morphological evolution at species range margins.

Keywords: Developmental instability, absent tooth, connate tooth, abnormal shaped tooth, *Euroscaptor*, *Mogera*.

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*Corresponding author email: tuanhai@eulipotlyphla.com

INTRODUCTION

While dental anomalies are rare in most mammals (Feldhamer et al., 2020), they are a concern in moles because their dental formulas are crucial for genus classification within Talpidae, and their high prevalence of these anomalies in the subterranean moles has evolutionary implications (Stein, 1962; Motokawa, 2001; Kawada et al., 2006, 2011; Asahara et al., 2012; Okabe et al., 2021). Dental variations among mole genera are found commonly in incisor and pre-molar rows of moles in Talpidae (Ueda, 1959; Ziegler, 1971; Abe et al., 1991; Kryštufek et al., 2001; Motokawa et al., 2001; Kawada et al., 2006), which were not seen in some rodents (for instances, Sone et al., 2004). Hence, species in Talpini become potential objects to study dental anomalies.

According to Abe et al. (1991), dental anomalies of Japanese moles were very rare, and they situated this fact to certificate the new genus, *Nesosaptor*, with a different tooth number from Uotsuri Island, Ryukyu, Japan. After that, Motokawa et al. (2001) described the dental variation in Taiwanese ally of Japanese moles and the Taiwanese mole, *Mogera insularis*, showed a greater frequency of dental number. Thus, they considered *Nesosaptor* to be a junior synonym of *Mogera* based on their observation. The morphological characteristics of the incisors and canines distinguish the Talpinae tribes, including the Talpini, where the upper canine is notably larger than the incisors (Kryštufek & Motokawa, 2018; Okabe et al., 2021).

Dental anomalies in Talpini have been found primarily in premolars, consisting mostly of absent premolars, with connate and extra premolars accounting for a smaller proportion (Kryštufek et al., 2001; Kawada et al., 2006, 2011; Feldhamer & Towery, 2011; Asahara et al., 2012; Okabe et al., 2021; Okabe, 2024).

Southeast Asia, a hotspot of talpid diversity, remains a significant gap in our understanding of dental morphology and variation (Shinohara

et al., 2014). The region's complex biogeography, characterized by fragmented highland habitats, creates conditions conducive to population isolation, genetic drift, and potentially, elevated developmental instability (Kawada et al., 2009). Studies on other taxa suggest marginal populations often exhibit lower genetic variation and increased developmental abnormalities compared to central populations (Hardie & Hutchings, 2010; Pironon et al., 2017). This phenomenon, termed developmental instability, can manifest as random deviations from perfect bilateral symmetry, known as fluctuating asymmetry (FA), and is considered a sensitive indicator of genetic and environmental stress (Møller & Swaddle, 1997).

Previous morphological work on Vietnamese moles did not specifically address the frequency or nature of dental anomalies (Bui et al., 2020). Therefore, to address these inconsistencies and clarify patterns of dental anomalies in Vietnamese moles, we conducted a comprehensive examination of specimens from various geographic locations in Vietnam. We aimed to document the frequency, types, and distribution of dental anomalies based on the dental formulae proposed in prior research. Our findings provide new insights into patterns of dental anomalies in Talpini moles from Vietnam and their implications for understanding morphological evolution in this taxonomic group.

MATERIALS AND METHODS

We examined 148 skulls from seven species, including *Euroscaptor kuznetsovi* (n = 31), *Euroscaptor parvidens* (n = 25), *Euroscaptor ngoclinhensis* (n=36), *Euroscaptor orlovi* (n = 8), *Euroscaptor subanura* (n = 24), *Euroscaptor darwini* (n = 5) and *Mogera latouchei* (n = 19), collected from a wide range of their distributions from northern to southern Vietnam. All specimens were deposited at the Institute of Biology (IB), Vietnam Academy of Science and Technology (VAST). Detailed information about the studied specimens is presented in Appendix 1.

Anomaly identification and classification

The normal dentition of all *Euroscaptor* has a dental formula as I3/3, C1/1, P4/4, M3/3 = 44, *Mogera* as I3/2, C1/1, P4/4, M3/3 = 42 (I: incisor, C: canine, P: premolar, M: molar, upper/lower). We examined all specimens under a dissecting microscope (SMZ 745, Nikon, Japan) to identify anomalies, which were classified following established criteria (Kawada et al. 2006, 2011; Okabe et al. 2021; Okabe 2024). Anomaly categories included: Oligodonty (absent teeth), congenital absence confirmed by the lack of an alveolus; Connate teeth, fusion of two tooth germs; and Abnormally shaped teeth, including morphological (e.g., microdontia) and positional defects. Post-mortem tooth loss was excluded when remnants of roots or alveoli were present. This study is limited by the absence of X-ray imaging, preventing us from detecting embedded teeth (Natsume et al., 2005).

Craniodental and statistical analyses

We measured the skulls using a digital caliper (NTD12-15PMX, Mitutoyo, Japan) to the nearest 0.01 mm for the greatest length of the skull (GLS), palatal length (PL), and maxillary tooth row length (C-M3), following Bui et al. (2020). For statistical analysis, we performed descriptive statistics in PAST statistic 5.0 (Hammer et al., 2001), including

the arithmetic mean (M) and standard deviation (SD) for the measurements of all specimens and those with observed abnormalities. From the cranial morphometric index results, we analyzed the correlation coefficient (R^2) between the cranial morphometric index of the normal group (N) and that of the anomaly group (A). We applied a logarithmic function, $y = a \ln(x) + b$, to determine the correlation coefficient (R^2) between these two variables. We used a Chi-squared (χ^2) test of independence to compare the frequency of dental anomalies in our total sample with frequencies reported in published studies of other talpid populations. Independent samples t-tests were performed using PAST statistics 5.0 and Microsoft® Excel. A p-value of < 0.05 was considered statistically significant.

RESULTS

Of the 148 specimens examined, 15 (10.14%) exhibited one or more dental anomalies. Oligodonty was the most common defect, observed in 11 individuals (7.43% of the total sample), followed by abnormally shaped teeth ($n = 3$, 2.03%) and one case of a connate tooth ($n = 1$, 0.68%). The highest prevalence was found in *Euroscaptor ngoclinhensis* (16.67%) and *Euroscaptor parvidens* (16.00%). No anomalies were observed in *Euroscaptor orlovi* or *Euroscaptor darwini* (Table 1).

Table 1. Frequency and type of dental anomalies observed in seven mole species from Vietnam

Species	N	Anomalous specimens (%)	Oligodonty (%)	Connate tooth (%)	Abnormally shaped (%)
<i>Euroscaptor parvidens</i>	25	4 (16.00)	3 (12.00)	-	1 (4.00)
<i>Euroscaptor ngoclinhensis</i>	36	6 (16.67)	6 (16.67)	-	-
<i>Euroscaptor subanura</i>	24	1 (4.17)	1 (4.17)	-	-
<i>Euroscaptor kuznetsovi</i>	31	2 (6.45)	1 (3.23)	-	1 (3.23)
<i>Euroscaptor latouchei</i>	19	2 (10.53)	-	1 (5.26)	1 (5.26)
<i>Euroscaptor orlovi</i>	8	-	-	-	-
<i>Euroscaptor darwini</i>	5	-	-	-	-
Total	148	15 (10.14)	11 (7.43)	1 (0.68)	3 (2.03)

Anomalies were concentrated in the premolar region. All 11 cases of oligodonty involved the absence of one or more premolars, most commonly the second (P2/p2) and third (P3/p3) premolars (Figs. 1, 2). The single

connate tooth involved the fusion of the lower third and fourth premolars (p3-p4) in an *Mogera latouchei* specimen (Fig. 3). Abnormally shaped teeth included a case of mesial displacement of an upper incisor in *Euroscaptor parvidens*, an

extra space between I3 and C in *Euroscaptor kuznetsovi*, and microdontia of a lower premolar in *M. latouchei* (Fig. 4).

There were no statistically significant differences in the mean values of GLS, PL, or C-M3 between individuals with normal dentition and those with dental anomalies for any species analyzed (Table 2; independent samples t-tests, all $P > 0.05$). This indicates that the presence of dental anomalies was not associated with a reduction in overall skull size in our sample.



Figure 1. Bilateral oligodonty in *Euroscaptor subanura* (#SIK930), showing missing left upper and lower second premolars (P2 and p2)

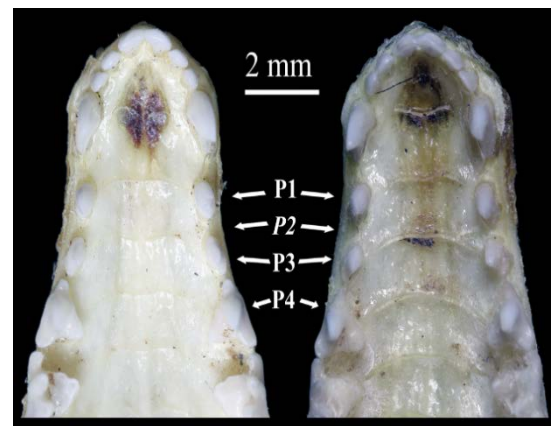


Figure 2. Bilateral oligodonty of the upper second premolar (P2) in *Euroscaptor ngoclinhensis*. (a) Specimen #NL09. (b) Specimen #NL07

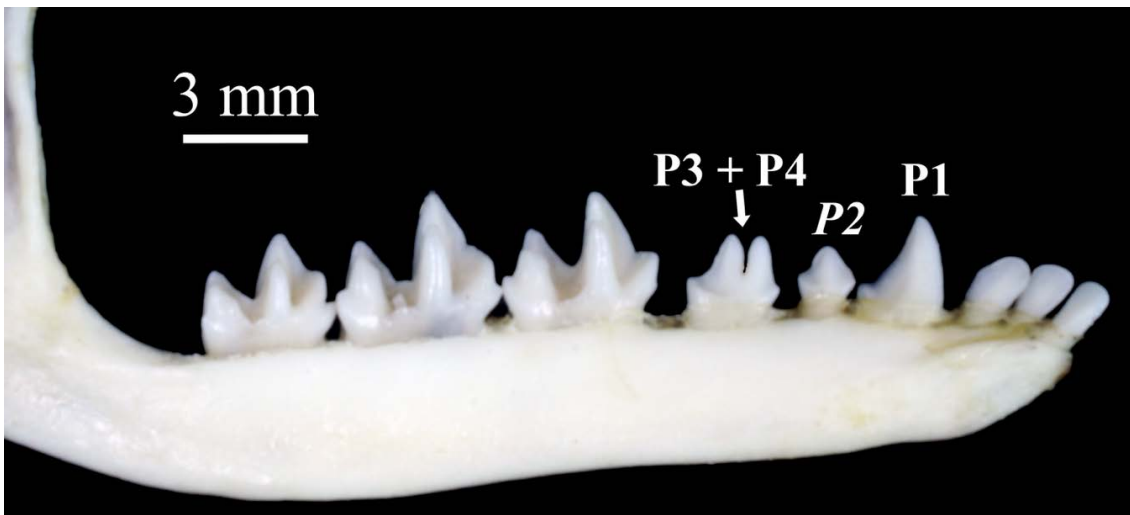


Figure 3. Morphological anomaly in *Mogera latouchei* (#SIK986), showing connate (fused) left lower third and fourth premolars (p3-p4)

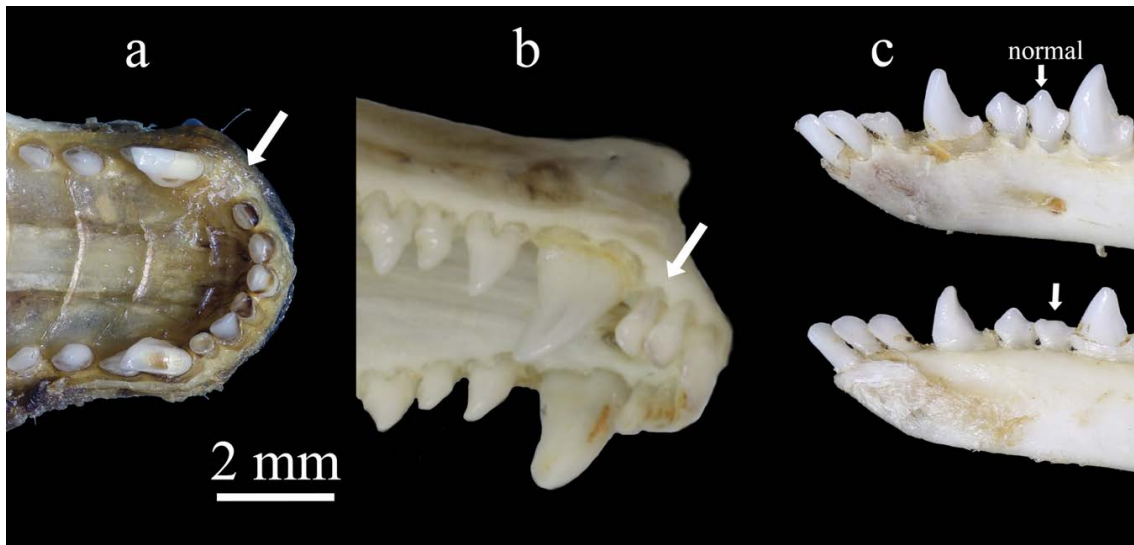


Figure 4. Examples of positional and morphological anomalies. (A) Positional anomaly in *Euroscaptor kuznetsovi*, showing mesial displacement of the left upper third incisor (I3). (B) Morphological anomaly (microdontia) in *Mogera latouchei*. (C) showing an abnormally small left lower third premolar (p3) compared to the normal contralateral tooth

Table 2. Comparison of craniodental measurements (mean $\pm$ SD, range) between total (T) and anomalous (D.A.) specimens. Results of independent samples t-tests show no significant differences ($P > 0.05$ for all comparisons). The measurements in total *Euroscaptor* spp. The specimens in our study were according to Bui et al. (2020)

Species	<i>Euroscaptor parvidens</i>			<i>Euroscaptor ngoclinhensis</i>			<i>Mogera latouchei</i>		
N (T/D.A)	25/4			36/6			19/2		
Mea.	GLS	PL	C-M3	GLS	PL	C-M3	GLS	PL	C-M3
T	33.34 ± 0.92 31.51– 34.70	12.95 $\pm$ 0.61 11.74– 13.95	10.75 $\pm$ 0.57 9.74– 11.66	31.90 $\pm$ 0.55 30.46– 32.81	12.25 $\pm$ 0.41 11.18– 12.61	9.92 $\pm$ 0.22 9.21– 10.30	30.10 $\pm$ 0.55 29.33– 31.38	12.06 $\pm$ 0.29 11.47– 12.56	10.46 ± 0.28 9.93– 11.01
D.A	34.24 ± 0.30 33.86– 34.70	13.55 $\pm$ 0.24 13.34– 13.95	10.92 $\pm$ 0.28 10.58– 11.36	32.05 $\pm$ 0.33 31.60– 32.46	12.37 $\pm$ 0.18 11.99– 12.55	9.89 $\pm$ 0.39 9.49– 10.64	30.61 $\pm$ 1.40 29.21– 32.01	12.00 $\pm$ 0.09 11.91– 12.08	9.79 $\pm$ 0.21 9.58– 10.00
t-test (df)	-1.91 (27)	-1.93 (27)	-0.58 (27)	-0.67 (40)	-0.71 (40)	0.20 (40)	-0.51 (19)	0.29 (19)	3.22 (19)
P-value	0.067	0.064	0.567	0.505	0.482	0.842	0.616	0.775	0.004*

*Note: A significant difference was found for C-M3 in *Mogera latouchei*, but with n=2 in the anomalous group, this result should be interpreted with extreme caution.

The correlation coefficient (R^2) between the craniodental measurements of the normal group and that of the anomaly group was showed in Figure 5. The analysis

revealed a strong correlation between the normal and anomaly groups with respect to the fundamental morphometric measurements.

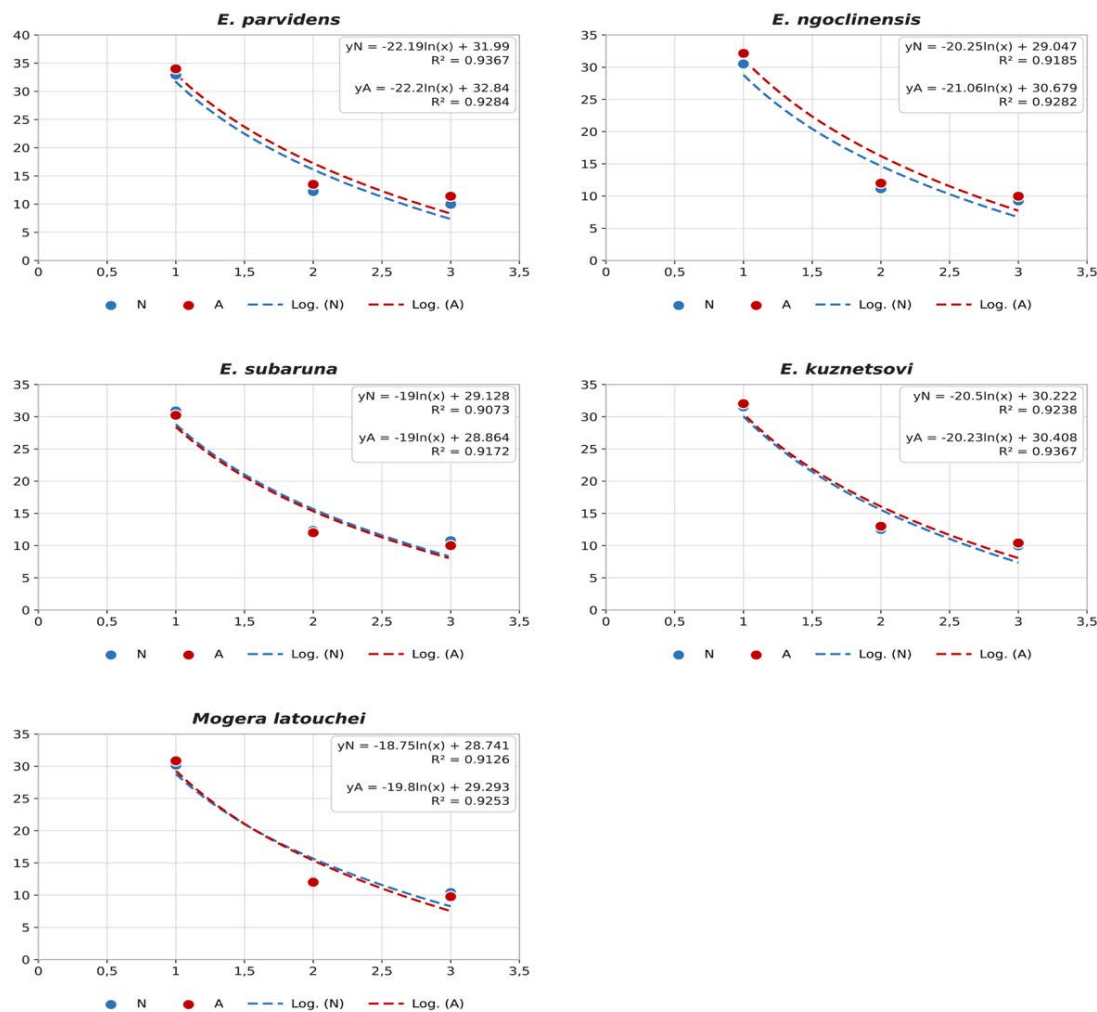


Figure 5. The correlation coefficient (R^2) between the cranial morphometric index of the normal group (N) and that of the anomaly group (A)

DICUSSION

This study provides the first quantitative assessment of dental anomalies in Vietnamese moles, revealing a prevalence of 10.14%. This rate is numerically higher than those reported in previous studies on *Mogera* species from Japan (6.7%, $n = 119$; Ueda, 1959; 6.43%, $n = 684$; Kawada et al., 2011) and significantly lower than that in *Talpa altaica* from Siberia (22.9%; Kawada et al., 2006), but higher than that in *Urotrichus talpoides* (1.7%; Okabe et al., 2021). These comparisons highlight notable interspecific and geographic variation within Talpidae, particularly between *Euroscaptor*, *Mogera*, *Talpa*, and *Urotrichus*. Statistical

comparisons among these groups did not show a significant overall difference (Table 3). However, at the species level, the 16.67% anomaly frequency in *E. ngoclinensis* was higher than that reported for *Mogera wogura*.

The specimens for this study were collected in Vietnam, which constitutes a southern peripheral area of the species' distribution range that extends from Peninsular Malaysia to southern China and the Himalayan region (Hutterer, 2005; Hoffmann & Lunde, 2008). This finding is consistent with the hypothesis that the frequency of dental anomalies increases in mammalian marginal populations (Asahara et al., 2012). Our central

hypothesis was that the high prevalence of anomalies could be attributed to the populations' marginal geographic position. Peripheral populations are often smaller, more isolated, and subject to stronger genetic drift, which can increase the frequency of deleterious alleles and disrupt developmental homeostasis (Kawecki, 2008; Hardie & Hutchings, 2010). While the link between marginality and anomaly frequency is a plausible correlation, our study provides a more direct, mechanistic test of this hypothesis. The significantly higher level of fluctuating asymmetry in individuals

with dental anomalies is strong evidence that these defects are not isolated events but rather manifestations of a systemic failure to buffer development against genetic and environmental perturbations. This finding directly links the observed dental phenotypes to the underlying process of developmental instability, providing quantitative support for the "marginal population" effect. The lack of association between anomalies and skull size further suggests that these are not simple allometric effects but are rooted in developmental pathways.

Table 3. Comparative frequency of dental anomalies in Talpidae populations and results of Chi-squared (χ^2) tests against the total Vietnamese sample

Species	Location	N	Anomaly Rate (%)	Primary Anomaly	Source	χ^2 (df = 1), P-value
<i>Euroscaptor</i> & <i>Mogera</i> spp.	Vietnam	148	10.14	Premolar Oligodonty	This study	-
<i>Euroscaptor ngoclinhensis</i>	Vietnam	36	16.67	Premolar Oligodonty	This study	1.89, P = 0.169
<i>Mogera wogura</i>	Japan	684	6.43	Premolar Oligodonty	Kawada et al. 2011	2.53, P = 0.112
<i>Talpa altaica</i>	Siberia	1789	22.9	Premolar Oligodonty	Kawada et al. 2006	14.50, P < 0.001
<i>Scalopus aquaticus</i>	North America	249	14.5	Incisor/Premolar Oligodonty	Feldhamer & Towery 2011	1.63, P = 0.202
<i>Urotrichus talpoides</i>	Japan	1001	1.7	Canine Oligodonty	Okabe et al. 2021	22.80, P < 0.001

The overwhelming predominance of premolar oligodonty in our sample points toward a specific, rather than random, developmental disruption. Extensive research in developmental genetics has identified the transcription factors *MSX1* and *PAX9* as critical regulators of odontogenesis. In both mice and humans, mutations in *MSX1* and *PAX9* are strongly and specifically associated with the agenesis of posterior teeth, including second premolars and molars (Vastardis et al., 1996; Stockton et al., 2000; Nieminen, 2009). The specific pattern of missing P2 and P3 teeth observed in Vietnamese *Euroscaptor* is the classic phenotype associated with haploinsufficiency of these genes.

We advance a more nuanced hypothesis: the fragmented, high-elevation habitats

occupied by these Vietnamese moles function as ecological islands that foster genetic drift. Such drift may have increased the prevalence of mildly deleterious variants within the highly conserved *MSX1/PAX9* signaling pathways. Although not lethal, these variants could perturb the precise signaling required for initiating specific tooth germs, thereby producing the unusually high frequency of premolar oligodonty. This scenario offers a concrete and biologically plausible mechanism linking a population-level process (habitat marginality and genetic drift) to an organismal-level phenotype (dental anomalies and developmental instability).

M. latouchei and *Euroscaptor* spp. have a close and complex genetic relationship. *Euroscaptor* divided about 12-13 million

years ago and as for *M. latouchei* it was about 10 million years ago, far later than *Euroscaptor* (Shinohara et al., 2014). Connate teeth is identified as the form of fusion between normal and supernumerary tooth germs or between two normal tooth. The occurrence of connate teeth is apparently frequent in the lower fourth premolar of moles which is stated in previous studies (Stein, 1962; Abe et al., 1991; Kawada et al., 2006). The single case of a connate p3–p4 in *M. latouchei* is also noteworthy. While a single observation precludes any macroevolutionary conclusions, it illustrates a potential developmental pathway for the evolutionary reduction in premolar number that distinguishes *Mogera* from *Euroscaptor*.

The relationship between skull size reduction and dental anomalies, particularly oligodonty has been debated. Some studies suggest a link, reporting this phenomenon in populations of *Scapanulus latimanus* (Hall, 1940) and *M. wogura* (Kawada et al., 2011). In contrast, other research indicates no such correlation. For example, skull size reduction in *Vulpes vulpes* was not linked to tooth loss, despite a high prevalence of dental anomalies in the population (Szuma, 2007; Szuma, 2008). Similarly, Asahara et al. (2012) found no association between skull size and the occurrence of dental anomalies. Our t-test likewise revealed no significant difference in size between the two groups. This result suggested that dental anomalies might not correspond to skull size. Several other studies also supported that oligodonty in Eulipotyphla is the result of genetic factors instead of skull sizes in the cases of mice (Line, 2003), *Suncus murinus* (Jogahara et al., 2007) and *Mogera* (Asahara et al., 2012).

CONCLUSION

This study demonstrates a high prevalence of dental anomalies, primarily premolar oligodonty, in Vietnamese mole populations. We provide the first quantitative evidence linking these anomalies to increased developmental instability, as indicated by elevated fluctuating asymmetry. These findings support the hypothesis that genetic

stress associated with range-edge populations may disrupt developmental homeostasis. Furthermore, the observed pattern of tooth loss is consistent with perturbations in conserved odontogenetic pathways regulated by key developmental genes such as *MSX1* and *PAX9*. Collectively, these populations represent a valuable natural system for exploring the interactions among population genetics, developmental stability, and the evolution of mammalian dentition. Future research integrating genomic analysis of candidate odontogenetic genes with expanded geographic sampling will be essential to further test and refine these hypotheses.

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REFERENCES

- Abe H., Shiraishi S., Arai S., 1991. A new mole from Utsurijima, the Ryukyu Islands. *Journal of the Mammalogical Society of Japan*, 16(1): 47–60.
- Asahara M., Kryukov A., Motokawa M., 2012. Dental anomalies in the Japanese mole *Mogera wogura* from northeast China and the Primorsky region of Russia. *Acta Theriologica*, 57: 41–48. <https://doi.org/10.1007/s13364-011-0050-0>
- Bui H.T., Motokawa, Kawada S., Abramov A.V., Nguyen S. T., 2020. Skull variation in Asian moles of the genus *Euroscaptor* (Eulipotyphla: Talpidae) in Vietnam. *Mammal Study*, 45(4): 265–280. <https://doi.org/10.3106/ms2019-0058>
- Feldhamer A. G., Merritt F. J., Krajewski C., Rachlow L. J. and Stewart M. K., 2020. *Mammalogy*, Fifth edition. Johns Hopkins University Press, Baltimore, pp. 725
- Feldhamer A. G., and Towery N. B., 2011. Dental anomalies in the Eastern Mole (*Scalopus aquaticus*). *The American Midland Naturalist*, 165(2): 421–425. <https://doi.org/10.1674/0003-0031-165.2.421>

- 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(2): 103–143. <https://doi.org/10.1177/00220345400190020>
- Hammer Ø., Harper D. A. T. and Ryan P. D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4: 1–9.
- Hardie D. C., Hutchings J. A., 2010. Evolutionary ecology at the extremes of species's ranges. *Environmental Review*, 18: 1–20. <https://doi.org/10.1139/A09-014>
- Hoffmann R. S., Lunde D., 2008. Order Soricomorpha. In: Smith A. T., Xie Y. (eds). A guide to the mammals of China. Princeton University Press, Princeton, pp. 297–326.
- Hutterer R., 2005. Order Soricomorpha. Pp. 220–311 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- Jogahara T., Koyasu K., Oda S., Kawai T., Hanamura H., 2007. Quest for the cause of oligodontia in *Suncus murinus* (Soricomorpha, Soricidae): morphological re-examination. *Archives of Oral Biology*, 52(9): 836–843. <https://doi.org/10.1016/j.archoralbio.2007.01.011>
- Kawada S., Koyasu K., Zholnerovskaya E. I., Oda S., 2006. Analysis of dental anomalies in the Siberian mole, *Talpa altaica* (Insectivora, Talpidae). *Archives of Oral Biology*, 51(11): 1029–1039. <https://doi.org/10.1016/j.archoralbio.2006.04.011>
- Kawada S., Endo H., Oda S., and Koyasu K., 2011. Dental Anomalies in Four Mole Species of the Genus *Mogera* (Insectivora, Talpidae) from Japan. *Bull. Natl. Mus. Nat. Sci., Ser. A*, 37(1): 63–72.
- Kawecki T. J., 2008. Adaptation to marginal habitats. *Annu Rev Ecol Evol Sys*, 39: 321–342. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095622>
- Krystufek B., Spitzenberger F., Kefelioglu H., 2001. Description, taxonomy, and distribution of *Talpa davidiana*. *Mamm Biol* 66(3): 135–143.
- Line S., 2003. Variation of tooth number in mammalian dentition: connecting genetics, development, and evolution. *Evol Dev*, 5: 295–304. <https://doi.org/10.1046/j.1525-142X.2003.03036.x>
- Motokawa M., Lin L. K., Cheng H. C., Harada M., 2001. Taxonomic status of the Senkaku mole, *Nesoscaplor uchidai*, with special reference to variation in *Mogera insularis* from Taiwan (Mammalia: Insectivora). *Zoological Science*, 18(5): 733–740. <https://doi.org/10.2108/zsj.18.733>
- Møller A. P. & Swaddle J. P., 1997. Asymmetry developmental stability, and evolution. Oxford University Press, UK, pp. 292.
- Natsume A., Koyasu K., Hanamura H., Nakagaki H., and Oda S., 2005. Variations in the number of teeth in wild Japanese serow (*Naemorhedus crispus*). *Archives of Oral Biology*, 50(10): 849–860. <https://doi.org/10.1016/j.archoralbio.2004.12.011>
- Nieminen P., 2009. Genetic basis of tooth agenesis. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 312B: 320–342. <https://doi.org/10.1002/jez.b.21277>
- Okabe S., 2024. Dental Anomalies in the Lesser Japanese Shrew-Mole *Dymecodon pilirostris* (Mammalia, Talpidae), with the First Record of an Extra Tooth. *Bull. Natl. Mus. Nat. Sci., Ser. A*, 50(4): 193–197.
- Okabe S., Shinohara A., Motokawa M., 2021. New dental anomalies in the greater Japanese shrew mole *Urotrichus talpoides* (Eulipotyphla: Talpidae). *Mammal Study*, 46: 309–315.
- Pironon S., Papuga G., Villellas J., Angert A. L., García M. B., Thomson J. D., 2017.

- Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. *Biological reviews*, 92(4): 1877–1909. <https://doi.org/10.1111/brev.12313>
- Shinohara A., Kawada S., Son N. T., Can D. N., Endo H, Suzuki H. and Koshimoto C., 2014. Molecular phylogenetic of East and Southeast Asian fossorial moles (Lipotyphla, Talpidae). *Journal of Mammalogy*, 95(3): 455–466. <https://doi.org/10.1644/13-MAMM-A-135>
- Sone K., Koyasu K. and Oda S., 2004. Dental and skull anomalies in feral coypu, *Myocastor coypus*. *Archives of Oral Biology*, 49(10): 849–854. <https://doi.org/10.1016/j.archoralbio.2004.02.015>
- 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).
- Stockton D. W., Das M. P., Goldenberg R. D, Souza N., and Patel P. K., 2000. Mutation of PAX9 is associated with oligodontia. *Nature Genetics*, 24: 18–19. <https://doi.org/10.1038/71634>
- Szuma E., 2007. Geography of dental polymorphism in the red fox *Vulpes vulpes* and its evolutionary implications. *Bioi J Linn Soc*, 90: 61–84. <https://doi.org/10.1111/j.1095-8312.2007.00712.x>
- SZuma E., 2008. Evolutionary and climatic factors affecting tooth size in the red fox *Vuples vulpes* in the Holarctic. *Acta Theriol*, 53: 289–332. <https://doi.org/10.1007/BF03195193>
- Ueda Y., 1959. About dental anomalies of moles. *Hiroshima Daigaku Igakubu Kaibougaku Daiichikouza Gyousekisyu*, 5: 1–6. (In Japanese)
- Vastardis H., Karimbux N., Guthua S. W., Seidman T. J., and Seidman C. E., 1996. A human MSX1 homeodomain missense mutation causes selective tooth agenesis. *Nature Genetics*, 13: 417–421. <https://doi.org/10.1038/ng0896-417>
- Ziegler A. C., 1971. Dental homologies and possible relationships of recent Talpidae. *Journal of Mammalogy*, 52: 50–68. <https://doi.org/10.2307/1378431>

Appendix 1. List of the specimens examined in the present study

No.	Species	Voucher	Locality
1	<i>Euroscaptor kuznetsovi</i>	SIK774	Tam Dao, Phu Tho
2	<i>Euroscaptor kuznetsovi</i>	SIK775	Tam Dao, Phu Tho
3	<i>Euroscaptor kuznetsovi</i>	SIK776	Tam Dao, Phu Tho
4	<i>Euroscaptor kuznetsovi</i>	SIK777	Tam Dao, Phu Tho
5	<i>Euroscaptor kuznetsovi</i>	SIK778	Tam Dao, Phu Tho
6	<i>Euroscaptor kuznetsovi</i>	SIK779	Tam Dao, Phu Tho
7	<i>Euroscaptor kuznetsovi</i>	SIK781	Tam Dao, Phu Tho
8	<i>Euroscaptor kuznetsovi</i>	SIK788	Tam Dao, Phu Tho
9	<i>Euroscaptor kuznetsovi</i>	CB16	Nguyen Binh, Cao Bang
10	<i>Euroscaptor kuznetsovi</i>	SIK865	Nguyen Binh, Cao Bang
11	<i>Euroscaptor kuznetsovi</i>	SIK866	Nguyen Binh, Cao Bang
12	<i>Euroscaptor kuznetsovi</i>	SIK867	Nguyen Binh, Cao Bang
13	<i>Euroscaptor kuznetsovi</i>	NB003	Nguyen Binh, Cao Bang
14	<i>Euroscaptor kuznetsovi</i>	SIK967	Khau Ca, Tuyen Quang
15	<i>Euroscaptor kuznetsovi</i>	SIK969	Khau Ca, Tuyen Quang
16	<i>Euroscaptor kuznetsovi</i>	Motokawa 0988	Tay Con Linh, Tuyen Quang

No.	Species	Voucher	Locality
17	<i>Euroscaptor kuznetsovi</i>	Motokawa 1004	Tay Con Linh, Tuyen Quang
18	<i>Euroscaptor kuznetsovi</i>	Motokawa 1029	Tay Con Linh, Tuyen Quang
19	<i>Euroscaptor kuznetsovi</i>	TCL 05.2017-04	Tay Con Linh, Tuyen Quang
20	<i>Euroscaptor kuznetsovi</i>	TCL 05.2017-05	Tay Con Linh, Tuyen Quang
21	<i>Euroscaptor kuznetsovi</i>	TCL 05.2017-06	Tay Con Linh, Tuyen Quang
22	<i>Euroscaptor kuznetsovi</i>	TCL 05.2017-07	Tay Con Linh, Tuyen Quang
23	<i>Euroscaptor kuznetsovi</i>	TCL 05.2017-08	Tay Con Linh, Tuyen Quang
24	<i>Euroscaptor kuznetsovi</i>	TCL 05.2017-09	Tay Con Linh, Tuyen Quang
25	<i>Euroscaptor kuznetsovi</i>	81.01	Tay Con Linh, Tuyen Quang
26	<i>Euroscaptor kuznetsovi</i>	81.02	Tay Con Linh, Tuyen Quang
27	<i>Euroscaptor kuznetsovi</i>	81.03	Tay Con Linh, Tuyen Quang
28	<i>Euroscaptor kuznetsovi</i>	81.04	Tay Con Linh, Tuyen Quang
29	<i>Euroscaptor kuznetsovi</i>	81.05	Tay Con Linh, Tuyen Quang
30	<i>Euroscaptor kuznetsovi</i>	NTS 2019.10	Bac Me, Tuyen Quang
31	<i>Euroscaptor kuznetsovi</i>	NTS 2023-17	Na Hang, Tuyen Quang
32	<i>Euroscaptor orlovi</i>	Motokawa 0846	Fansipan, Lao Cai
33	<i>Euroscaptor orlovi</i>	Motokawa 0980	Fansipan, Lao Cai
34	<i>Euroscaptor orlovi</i>	Motokawa 0981	Fansipan, Lao Cai
35	<i>Euroscaptor orlovi</i>	Motokawa 0982	Fansipan, Lao Cai
36	<i>Euroscaptor orlovi</i>	Motokawa 1017	Fansipan, Lao Cai
37	<i>Euroscaptor orlovi</i>	Motokawa 1018	Fansipan, Lao Cai
38	<i>Euroscaptor orlovi</i>	Motokawa 1019	Fansipan, Lao Cai
39	<i>Euroscaptor orlovi</i>	Motokawa 1020	Fansipan, Lao Cai
40	<i>Euroscaptor subanura</i>	XN16	Xuan Nha, Son La
41	<i>Euroscaptor subanura</i>	XN20	Xuan Nha, Son La
42	<i>Euroscaptor subanura</i>	XN58	Xuan Nha, Son La
43	<i>Euroscaptor subanura</i>	XN61	Xuan Nha, Son La
44	<i>Euroscaptor subanura</i>	XN62	Xuan Nha, Son La
45	<i>Euroscaptor subanura</i>	Motokawa 0518	Xuan Lien, Thanh Hoa
46	<i>Euroscaptor subanura</i>	SIK875	Tam Dao, Phu Tho
47	<i>Euroscaptor subanura</i>	SIK876	Tam Dao, Phu Tho
48	<i>Euroscaptor subanura</i>	SIK883	Tam Dao, Phu Tho
49	<i>Euroscaptor subanura</i>	SIK884	Tam Dao, Phu Tho
50	<i>Euroscaptor subanura</i>	SIK888	Tam Dao, Phu Tho
51	<i>Euroscaptor subanura</i>	SIK889	Tam Dao, Phu Tho
52	<i>Euroscaptor subanura</i>	SIK890	Tam Dao, Phu Tho
53	<i>Euroscaptor subanura</i>	SIK930	Xuan Son, Phu Tho
54	<i>Euroscaptor subanura</i>	SIK931	Xuan Son, Phu Tho
55	<i>Euroscaptor subanura</i>	SIK932	Xuan Son, Phu Tho
56	<i>Euroscaptor subanura</i>	SIK933	Xuan Son, Phu Tho
57	<i>Euroscaptor subanura</i>	SIK934	Xuan Son, Phu Tho
58	<i>Euroscaptor subanura</i>	SIK935	Xuan Son, Phu Tho
59	<i>Euroscaptor subanura</i>	SIK936	Xuan Son, Phu Tho
60	<i>Euroscaptor subanura</i>	SIK937	Xuan Son, Phu Tho
61	<i>Euroscaptor subanura</i>	SIK938	Xuan Son, Phu Tho

No.	Species	Voucher	Locality
62	<i>Euroscaptor subanura</i>	SIK939	Xuan Son, Phu Tho
63	<i>Euroscaptor subanura</i>	NTS.2018.09.01	Na Hang, Tuyen Quang
64	<i>Euroscaptor ngoclinhensis</i>	BTH2	Bac Huong Hoa, Quang Tri
65	<i>Euroscaptor ngoclinhensis</i>	Motokawa 0637	Ngoc Linh, Quang Ngai
66	<i>Euroscaptor ngoclinhensis</i>	Motokawa 0641	Ngoc Linh, Quang Ngai
67	<i>Euroscaptor ngoclinhensis</i>	Motokawa 0642	Ngoc Linh, Quang Ngai
68	<i>Euroscaptor ngoclinhensis</i>	SIK850	Dong Giang, Da Nang
69	<i>Euroscaptor ngoclinhensis</i>	SIK855	Dong Giang, Da Nang
70	<i>Euroscaptor ngoclinhensis</i>	SIK856	Dong Giang, Da Nang
71	<i>Euroscaptor ngoclinhensis</i>	SIK857	Dong Giang, Da Nang
72	<i>Euroscaptor ngoclinhensis</i>	SIK858	Dong Giang, Da Nang
73	<i>Euroscaptor ngoclinhensis</i>	SIK859	Dong Giang, Da Nang
74	<i>Euroscaptor ngoclinhensis</i>	SIK860	Dong Giang, Da Nang
75	<i>Euroscaptor ngoclinhensis</i>	SIK861	Dong Giang, Da Nang
76	<i>Euroscaptor ngoclinhensis</i>	SIK862	Dong Giang, Da Nang
77	<i>Euroscaptor ngoclinhensis</i>	SIK863	Dong Giang, Da Nang
78	<i>Euroscaptor ngoclinhensis</i>	SIK864	Dong Giang, Da Nang
79	<i>Euroscaptor ngoclinhensis</i>	SIK853	Chu Yang Sin, Dak Lak
80	<i>Euroscaptor ngoclinhensis</i>	SIK970	Bac Huong Hoa, Quang Tri
81	<i>Euroscaptor ngoclinhensis</i>	SIK971	Bac Huong Hoa, Quang Tri
82	<i>Euroscaptor ngoclinhensis</i>	SIK972	Bac Huong Hoa, Quang Tri
83	<i>Euroscaptor ngoclinhensis</i>	SIK973	Bac Huong Hoa, Quang Tri
84	<i>Euroscaptor ngoclinhensis</i>	SIK974	Bac Huong Hoa, Quang Tri
85	<i>Euroscaptor ngoclinhensis</i>	SIK975	Bac Huong Hoa, Quang Tri
86	<i>Euroscaptor ngoclinhensis</i>	SIK976	Bac Huong Hoa, Quang Tri
87	<i>Euroscaptor ngoclinhensis</i>	IEBR M 7440	Kon Ka Kinh, Gia Lai
88	<i>Euroscaptor ngoclinhensis</i>	M bato190413.5	Ba To, Quang Ngai
89	<i>Euroscaptor ngoclinhensis</i>	M bato190413.6	Ba To, Quang Ngai
90	<i>Euroscaptor ngoclinhensis</i>	BTQN03	Ba To, Quang Ngai
91	<i>Euroscaptor ngoclinhensis</i>	BTQN04	Ba To, Quang Ngai
92	<i>Euroscaptor ngoclinhensis</i>	BTQN06	Ba To, Quang Ngai
93	<i>Euroscaptor ngoclinhensis</i>	BTQN07	Ba To, Quang Ngai
94	<i>Euroscaptor ngoclinhensis</i>	BTQN08	Ba To, Quang Ngai
95	<i>Euroscaptor ngoclinhensis</i>	BTQN09	Ba To, Quang Ngai
96	<i>Euroscaptor ngoclinhensis</i>	BTH14-113	Ngoc Linh, Quang Ngai
97	<i>Euroscaptor ngoclinhensis</i>	nts2019.n.2.11	Ngoc Linh, Quang Ngai
98	<i>Euroscaptor ngoclinhensis</i>	NL07	Ngoc Linh, Quang Ngai
99	<i>Euroscaptor ngoclinhensis</i>	NL09	Ngoc Linh, Quang Ngai
100	<i>Euroscaptor parvidens</i>	CYS36	Chu Yang Sin, Dak Lak
101	<i>Euroscaptor parvidens</i>	CYS39	Chu Yang Sin, Dak Lak
102	<i>Euroscaptor parvidens</i>	SIK0852	Chu Yang Sin, Dak Lak
103	<i>Euroscaptor parvidens</i>	SIK0854	Chu Yang Sin, Dak Lak
104	<i>Euroscaptor parvidens</i>	Motokawa 0420	Hon Ba, Khanh Hoa
105	<i>Euroscaptor parvidens</i>	Motokawa 0421	Hon Ba, Khanh Hoa
106	<i>Euroscaptor parvidens</i>	Motokawa 0427	Hon Ba, Khanh Hoa

No.	Species	Voucher	Locality
107	<i>Euroscaptor parvidens</i>	Motokawa 0428	Hon Ba, Khanh Hoa
108	<i>Euroscaptor parvidens</i>	Motokawa 0429	Hon Ba, Khanh Hoa
109	<i>Euroscaptor parvidens</i>	Motokawa 0430	Hon Ba, Khanh Hoa
110	<i>Euroscaptor parvidens</i>	Motokawa 0432	Hon Ba, Khanh Hoa
111	<i>Euroscaptor parvidens</i>	Motokawa 0433	Hon Ba, Khanh Hoa
112	<i>Euroscaptor parvidens</i>	Motokawa 0434	Hon Ba, Khanh Hoa
113	<i>Euroscaptor parvidens</i>	Motokawa 0435	Hon Ba, Khanh Hoa
114	<i>Euroscaptor parvidens</i>	Motokawa 0436	Hon Ba, Khanh Hoa
115	<i>Euroscaptor parvidens</i>	Motokawa 0437	Hon Ba, Khanh Hoa
116	<i>Euroscaptor parvidens</i>	Motokawa 0438	Hon Ba, Khanh Hoa
117	<i>Euroscaptor parvidens</i>	Motokawa 0439	Hon Ba, Khanh Hoa
118	<i>Euroscaptor parvidens</i>	Motokawa 0440	Hon Ba, Khanh Hoa
119	<i>Euroscaptor parvidens</i>	SIK0944	Da Lat, Lam Dong
120	<i>Euroscaptor parvidens</i>	SIK0945	Da Lat, Lam Dong
121	<i>Euroscaptor parvidens</i>	SIK0946	Da Lat, Lam Dong
122	<i>Euroscaptor parvidens</i>	NNU2017.02	Nam Nung, Dak Lak
123	<i>Euroscaptor parvidens</i>	NNU2017.05	Nam Nung, Dak Lak
124	<i>Euroscaptor parvidens</i>	NNU2017.09	Nam Nung, Dak Lak
125	<i>Euroscaptor darwini</i>	NTS.2024.PL.01	Pu Luong, Thanh Hoa
126	<i>Euroscaptor darwini</i>	NTS.2024.PL.02	Pu Luong, Thanh Hoa
127	<i>Euroscaptor darwini</i>	NTS.2024.PL.03	Pu Luong, Thanh Hoa
128	<i>Euroscaptor darwini</i>	NTS.2024.PL.04	Pu Luong, Thanh Hoa
129	<i>Euroscaptor darwini</i>	NTS.2024.PL.05	Pu Luong, Thanh Hoa
130	<i>Mogera latouchei</i>	SIK823	Sapa, Lao Cai
131	<i>Mogera latouchei</i>	SIK824	Sapa, Lao Cai
132	<i>Mogera latouchei</i>	SIK825	Sapa, Lao Cai
133	<i>Mogera latouchei</i>	SIK871	Nguyen Binh, Cao Bang
134	<i>Mogera latouchei</i>	SIK872	Nguyen Binh, Cao Bang
135	<i>Mogera latouchei</i>	SIK874	Nguyen Binh, Cao Bang
136	<i>Mogera latouchei</i>	SIK886	Nguyen Binh, Cao Bang
137	<i>Mogera latouchei</i>	SIK887	Nguyen Binh, Cao Bang
138	<i>Mogera latouchei</i>	CB16	Nguyen Binh, Cao Bang
139	<i>Mogera latouchei</i>	CB19	Nguyen Binh, Cao Bang
140	<i>Mogera latouchei</i>	NB003	Nguyen Binh, Cao Bang
141	<i>Mogera latouchei</i>	SIK893	Sin Ho, Lai Chau
142	<i>Mogera latouchei</i>	SIK894	Sin Ho, Lai Chau
143	<i>Mogera latouchei</i>	SIK895	Sin Ho, Lai Chau
144	<i>Mogera latouchei</i>	SIK896	Sin Ho, Lai Chau
145	<i>Mogera latouchei</i>	SIK898	Sin Ho, Lai Chau
146	<i>Mogera latouchei</i>	SIK899	Sin Ho, Lai Chau
147	<i>Mogera latouchei</i>	SIK968	Khau Ca, Tuyen Quang
148	<i>Mogera latouchei</i>	AVA 13-103	Ta Xua, Son La