ISSN 0012-4966, Doklady Biological Sciences, 2026, Vol. 528, pp. 119–124. © Pleiades Publishing, Ltd., 2026.
ISSN 0012-4966, Doklady Biological Sciences, 2026. © Pleiades Publishing, Ltd., 2026.

First Find of Late Pleistocene Remains of the Collared Lemming (*Dicrostonyx torquatus*, Pallas 1779) in the South of the Russian Far East

A. E. Gusev[a],* and M. P. Tiunov[a]

Presented by academician V.P. Bulgakov

Received March 13, 2026; revised March 31, 2026; accepted April 2, 2026

Abstract—Fossil remains of a collared lemming (*Dicrostonyx*) are described for the first time from the Late Pleistocene site of Perspektivnaya Cave (Primorsky krai). Radiocarbon dating places the finds within the MIS 2 period. Morphotype analysis of the first upper molars (M1 and M2) identified the population as *Dicrostonyx torquatus*. These data refine our understanding of the species' range and chronology, indicating a more southerly distribution and an earlier presence of *D. torquatus* in the Late Pleistocene than previously recognized.

Keywords: *Dicrostonyx torquatus*, Late Pleistocene, Perspektivnaya Cave, Primorsky krai, molars

DOI: 10.1134/S0012496626600107

Currently, only one species from the genus *Dicrostonyx* Gloger, 1841 inhabits the continental part of Eurasia. This is *D. torquatus* Pallas, 1778, which is widely distributed in tundra and forest-tundra and feeds primarily on shoots, leaves, and bark of dwarf birch and willow. A finding of bone remains of the species in Late Pleistocene and Holocene deposits is always of considerable biostratigraphic interest because the occurrence of the collared lemming is typically associated with tundra-like landscapes and cold climatic conditions. It should be noted that the morphological transformation of molars in the phylogenetic lineage of collared lemmings exhibits a consistent directionality, which has been thoroughly documented in the scientific literature [1–13]. The key evolutionary trend is the increasing complexity of the chewing surface of the molars through the formation of additional elements, which is considered an adaptation to processing coarse plant matter [8].

In the Pleistocene of northern Eurasia, the genus *Dicrostonyx* was represented by a species complex including *D. gulielmi* Sanford, 1870; *D. henseli* Hinton, 1910; *D. simplicior* Fejfar, 1966; *D. renidens* Zazhigin, 1974; *D. okaensis* Alexandrova, 1982; *D. meridionalis* Smirnov et Borodin, 1986; and *D. torquatus*.

In current scientific debate regarding the taxonomy of the genus, different approaches can be traced. A widely recognized concept holds that Middle Pleistocene forms belong to *D. simplicior* (predominance of the "simplicior" morphotype of M1 and M2); Late Pleistocene forms, to *D. gulielmi* (predominance of the "henseli" morphotype); and modern populations, to *D. torquatus* (predominance of the "torquatus" morphotype) [4, 6, 8]. Within this classification, *D. henseli* and *D. gulielmi* are considered synonymous taxa.

An alternative position, presented by V.S. Zazhigin based on a study of collared lemmings from the Middle Pleistocene of Western Siberia [10], proposes a different systematic scheme. That is, Early Pleistocene forms are identified as *D. simplicior*; Middle Pleistocene forms, as *D. henseli*; and Late Pleistocene and modern forms, as *D. torquatus*. In this interpretation, *D. gulielmi* and *D. torquatus* are regarded as synonyms.

Despite the recognition of significant chronological and geographic variability in dental traits, which is associated with the wide distribution of species during particular epochs of the Pleistocene [1–14], this variability remains poorly studied for several regions and time periods. Until now, the southernmost locality of Late Pleistocene collared lemming remains was Sakhalin Island [14]. In 2023, during paleontological excavations at Perspektivnaya Cave (43°39′820″ N, 132°43′645″ E), new fossil material was obtained from an exploratory trench and found to contain collared lemming bone remains.

[a] *Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences, Vladivostok, Russia*
**e-mail: uraziosutoku@mail.ru*

Perspektivnaya Cave is located in Primorsky krai, in the southern part of Mikhailovsky District, within a limestone rock outcrop on a hillside, 20 m above the water's edge on the left bank of the Levaya Ilistaya River. Behind the cave entrance lies a small entrance grotto with a flat area covered by clayey deposits [15]. An exploratory trench (1.0 × 1.8 m) was excavated under the left wall of the grotto, adjacent to an archaeological excavation whose deposits formed during the Holocene [16]. The deposits exposed by the exploratory trench formed at the end of the Late Pleistocene.

At the Beta Analytic laboratory, two radiocarbon dates were obtained from unconsolidated cave deposits using accelerator mass spectrometry (AMS): 18 550 ± 60 BP (22 442 ± 73 cal BP, Beta-660120) and 17 510 ± 60 BP (21 136 ± 120 cal BP, Beta-660121). The dating was performed on scapulae of the willow ptarmigan *Lagopus lagopus* (Linnaeus, 1758), which were found at depths of 20–30 and 40–50 cm, respectively. Remains of small mammals found in the cave deposits accumulated during MIS 2, which is characterized as the coldest stage of the Late Pleistocene and was accompanied by drastic changes in vegetation composition [17, 18].

The modern vegetation cover of the study area is diverse. Its northern parts are occupied by cedar–spruce forests with the presence of Yezo spruce, whitebark fir, and Korean pine. Black fir–broadleaf forests are widespread on southern slopes, while the central part of the plateau is occupied by dark coniferous fir–spruce forests with an admixture of birch [19].

The small mammal fauna of Perspektivnaya Cave includes the Amur lemming (*Lemmus amurensis* Vinogradov, 1924), the wood lemming (*Myopus schisticolor* Liljeborg, 1844), the northern pika (*Ochotona hyperborea* Pallas, 1811), and the Khasan pika (*Tonomochota khasanensis* Tiunov et Gusev, 2021). Bone remains of *Eutamias sibiricus* (Laxmann, 1769), *Pteromys volans* (Linnaeus, 1758), *Myospalax psilurus* (Milne-Edwards, 1874), and *Apodemus* spp. were additionally found in small numbers.

The collared lemming bone remains we found in the cave deposits are distributed relatively evenly throughout the entire thickness. For this study, 56 fossil specimens were used, including fragments of upper and lower jaws, as well as isolated teeth. All material is stored in the Theriology Laboratory of the Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences.

The first upper molars M1 and M2 are the most informative for determining the evolutionary stages of collared lemmings. In contrast, the lower molars are characterized by high individual variability, which complicates taxonomic diagnosis [1–8]. A specialized method proposed for quantitative assessment of the development of morphological structures on M1 and M2 by Smirnov [8], has made these teeth the primary objects for phylogenetic reconstructions, and the present study is likewise focused on them.

The criterion for species identification is the predominance of one of three morphotypes on the first upper molars: simplicior (sim), henseli (hen), or torquatus (tor). The samples under study were accordingly assigned to one of three species: *D. simplicior*, *D. gulielmi*, or *D. torquatus*. Within the species, three morphs are distinguished, differing in the degree of morphotype dominance on M1 and M2. In addition to species, Smirnov has identified transitional forms with double species names, where the first name refers to the species according to the dominant morphotype [8].

For the M1 ($n = 6$) and M2 ($n = 6$) of collared lemmings from Perspektivnaya Cave, the predominance of the torquatus morphotype is characteristic, followed by henseli, and then simplicior (Fig. 1). The combined proportion of the torquatus morphotype on both teeth amounts to 150% (Fig. 2), which in turn is characteristic of morph 2 of modern *D. torquatus* [8]. Among the most well-known finds, the same morph was discovered in modern lemmings from the Yamal Peninsula, the Arctic coast of Central Siberia [9, 13, 14], and from unconsolidated deposits of Medvezhya Cave [9].

Analysis of the morphotypes of the remaining teeth revealed the following patterns. The upper third molars M3 are represented only by the simplicior and henseli morphotypes on both the lingual and labial sides (Fig. 2). Assessing the overall shape of M3, it is worth noting the predominance of the sim–hen morphotype over the sim–sim and hen–hen morphotypes. The majority of m1 specimens are represented by the typical hen–hen morphotype, but the simpler morphotypes sim–sim and sim–hen were also observed. In a single specimen, we identified the sim–tor morphotype. The henseli morphotype similarly predominates on the third lower molar (m3, $n = 3$). In contrast, m2 ($n = 11$) is characterized by the presence of only one morphotype, torquatus. Considering the distribution of the morphotypes of the upper and lower teeth as a whole, it does not differ significantly from that of the modern collared lemming [8, 12, 13]. A notable difference is only the absence of the more complex morphotypes on M3 and m1. This difference is directly related to the limited amount of material, and the observed morphotype distribution cannot therefore be considered fully representative. Nevertheless, our analysis of the tooth morphotypes from Perspektivnaya Cave revealed characteristics typical of modern *D. torquatus*. Together with the radiocarbon dates from the deposits where the teeth were found, the observation allows this identification to be considered justified.

Figure 3 presents the mean lengths and mean widths of the first and second upper molars in the specimens from Perspektivnaya Cave and in modern

Fig. 1. Occlusal surface of the (a–f) M1 and (g–l) M2 teeth of *D. torquatus* from Perspektivnaya Cave.

collared lemming populations from the Urals and the European North.

A comparative analysis of the upper molars revealed a tendency toward a reduction in the length of these teeth from Perspektivnaya Cave compared to modern populations [6, 7, 11]. The width of the molars showed no significant differences. Given the limited sample size and the overlap in ranges of indi-

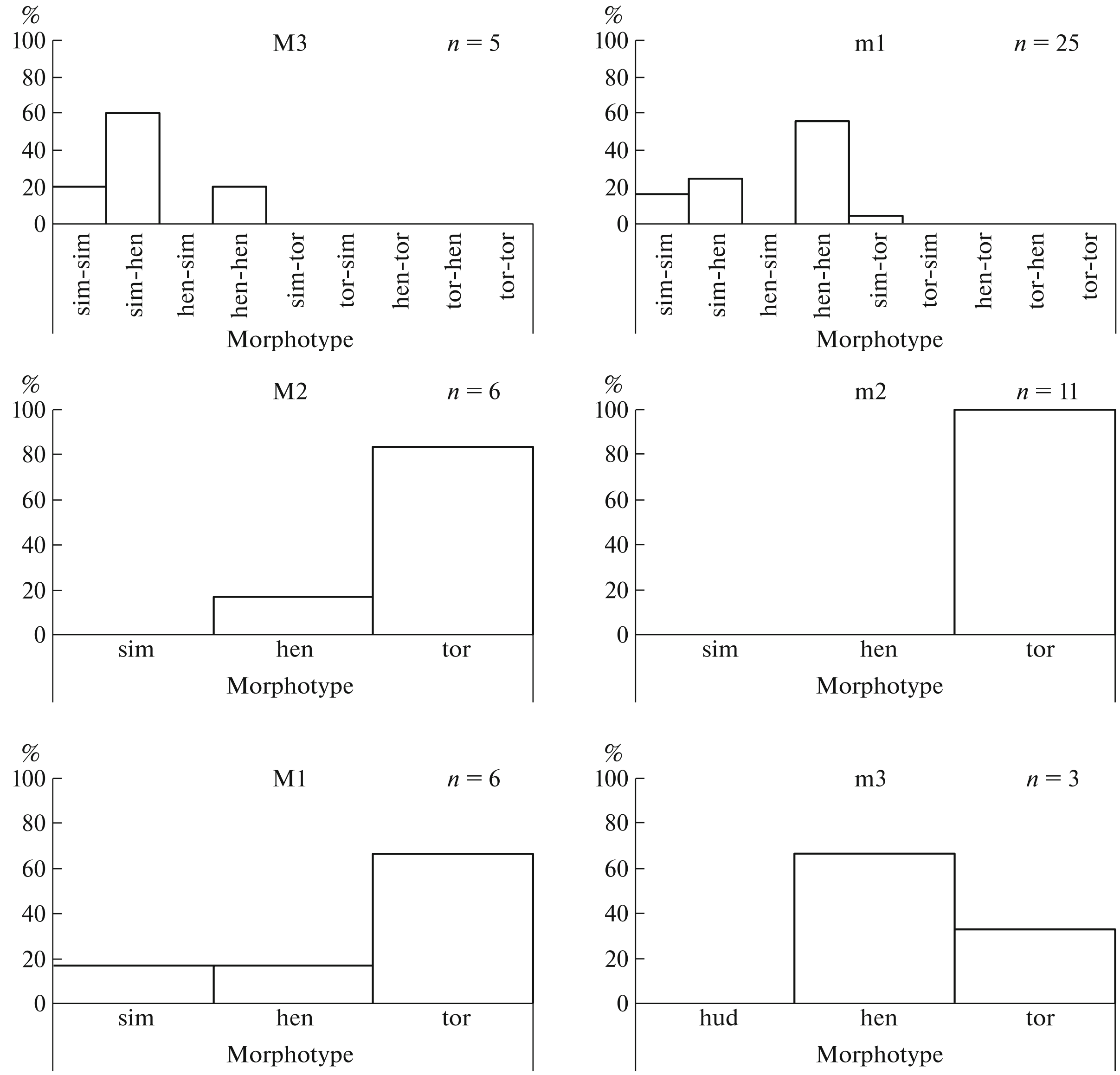

Fig. 2. Morphotype frequencies (%) in the samples of upper (M3, M2, and M1) and lower (m1, m2, and m3) teeth of collared lemmings from Perspektivnaya Cave. Abbreviations: sim, simplicior; hen, henseli; tor, torquatus; hud, hudsonius.

vidual variability, the observed differences require verification with more representative samples to assess their taxonomic or chronological significance.

The faunal assemblage of Perspektivnaya Cave is represented by species of cold landscapes and directly reflects the harsh paleoclimatic conditions of the Late Pleistocene in the south of the Russian Far East. In addition to the altitudinal zone shifts and the spread of tundra–taiga vegetation established from paleobotanical data [20], intense cryogenic processes could have been a key factor shaping the habitat for these animals. The lowering of the alpine belt boundary by 600–1000 m and the extensive development of talus slopes and stone runs created vast open rocky biotopes [20], analogous to modern habitats of the collared lemming in mountain tundras. Thus, the combination of a cool climate, specific vegetation, and characteristic mountainous terrain enabled the penetration and sustainable existence of periglacial fauna in the vicinity of Perspektivnaya Cave.

According to previously held views, the transition from *D. gulielmi* to *D. torquatus* occurred at the end of the Late Pleistocene, in the interval of approximately 15–13 thousand years ago [8, 9]. The *D. torquatus* fossil remains discovered in the south of the Russian Far East indicate an earlier appearance of the species in the paleontological record and a significant southward expansion of its range during the Late Pleistocene.

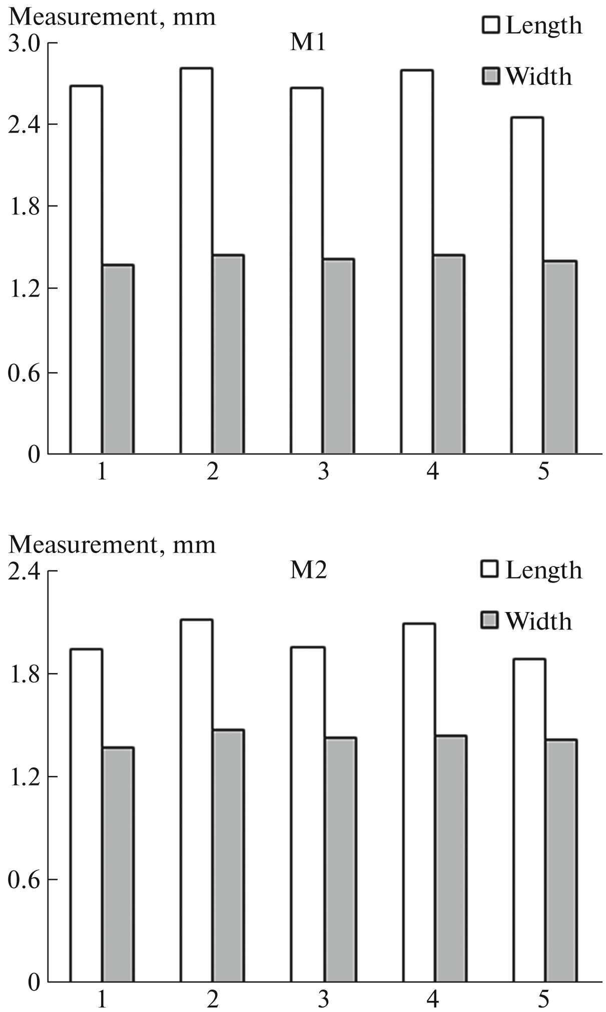

Fig. 3. Mean length and mean width of the first (M1) and second (M2) upper molars. Designations: 1, *D. torquatus*, Laya River basin [7]; 2, *D. torquatus*, Adzva River basin [7]; 3, *D. torquatus*, Pay-Khoy [7]; 4, *D. torquatus*, Yamal Peninsula [12]; 5, *D. torquatus*, Perspektivnaya Cave.

FUNDING

The work was carried out within the framework of a state assignment of the Ministry of Science and Higher Education of the Russian Federation (topic no. 124012200182-1).

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The study used only fossil materials. No work with live animals was conducted.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

1. Agadzhanyan, A.K., Lemming faunas of the Middle and Late Pleistocene, *Byull. Kom. Izuch. Chetvertichn. Perioda, Akad. Nauk SSSR*, 1972, no. 39, pp. 67–81.
2. Agadzhanyan, A.K., The history of the development of Arctic lemmings in the Pleistocene, in *Beringiya v kaynozoe* (Beringia in the Cenozoic), Vladivostok, 1976, pp. 289–295.
3. Zazhigin, V.S., Early stages of evolution of Arctic lemmings (Dicrostonychini, Microtinae, Rodentia) – typical representatives of the subarctic faunas of Beringia, in *Beringiya v kaynozoe* (Beringia in the Cenozoic), Vladivostok, 1976, pp. 280–288.
4. Nadachowski, A., *Late Quaternary Rodents of Poland with Special Reference to Morphotype Dentition Analysis of Voles*, Warszawa, Krakow: Panstwowe Wydawnictwo Naukowe, 1982.
5. Smirnov, N.G. and Bolshakov, V.N., The irregularity of the rates of complication of the dental system in collared lemmings, *Dokl. Biol. Sci.*, 1985, vol. 281, nos. 1–6, pp. 256–259.
6. Smirnov, N.G., Bolshakov, V.N., and Borodin, A.V., *Pleistotsenovye gryzuny severa Zapadnoi Sibiri* (Pleistocene Rodents of the Northern Part of Western Siberia), Moscow: Nauka, 1986.
7. Kochev, V.A., *Pleistotsenovye gryzuny severo-vostoka Evropeyskoy chasti Rossii i ikh stratigraficheskoe znachenie* (Pleistocene Rodents of the North-East of the European Part of Russia and their Stratigraphic Significance), St. Petersburg: Nauka, 1993.
8. Smirnov, N.G., Golovachev, I.B., Bachura, O.P., et al., *Slozhnyie sluchai opredeleniya zubov gryzunov iz otlozhenii pozdnego pleistotsena i golotsena tundrovyih raionov Severnoi Evrazii: Materialy po istorii i sovremennomu sostoyaniyu faunyi severa Zapadnoi Sibiri* (Complex Cases of Identification of Rodent Teeth from late Pleistocene and Holocene Deposits of the Tundra Regions of Northern Eurasia: Materials on the History and Current State of the Fauna of the North of Western Siberia), Chelyabinsk: Rifei, 1997, pp. 60–90.
9. Ponomarev, D. and Puzachenko, A., Evolution of occlusal shape of the first and second upper molars of Middle–Late Pleistocene collared lemmings (Dicrostonyx, Arvicolinae, Rodentia) in northeast European Russia, *Quat. Int.*, 2015, vol. 395, pp. 66–75. https://doi.org/10.1111/bor.12131
10. Zazhigin, V.S., On the Arctic lemmings (Dicrostonyx, Microtinae, Rodentia) of Oygos-Yar in Eastern Siberia and on the species status of the Middle Pleistocene species of the genus *Dicrostonyx*, in *Estestvennaya istoriya Rossiiskoi Vostochnoi Arktiki v pleistotsene i golotsene* (Natural History of Eastern Russian Arctic in the Pleistocene and Holocene), Nikolskiy, P.A., et al., Eds., Moscow: GEOS, 2003, pp. 14–26.
11. Borodin, A.V., *Opredelitel' zubov polevok Urala i Zapadnoi Sibiri* (*pozdnii pleistotsen – sovremennost*) (Guide for teeth of voles from Urals and Western Siberia (Late Pleistocene-Modern Times)), Yekaterinburg: Ural. Otd. Ross. Akad. Nauk, 2009.
12. Abramson, N.I., Smirnov, N.G., and Tikhonova, E.P., Morphological studies on collared lemmings (Rodentia, Arvicolidae, Dicrostonyx) from Bolshevik Island of

the Severnaya Zemlya Archipelago, with notes on evolution and taxonomic position, *Russ. J. Theriol.*, 2004, vol. 3, no. 2, pp. 63–70.
https://doi.org/10.15298/rusjtheriol.03.2.03

13. Kryazheva, I.V., New data on the faunal history of small herbivorous mammals in the Northern Urals during the Late Glacial and Holocene, *Vestn. Geonauk*, 2023, vol. 3, no. 339, pp. 11–22.
https://doi.org/10.19110/geov.2023.3.2
14. Kirillova, I.V. and Tesakov, A.S., Remains of gophers in the late Pleistocene deposits of the Ostantovaya Cave (Sakhalin Island), *Materialy rossiiskoi nauchnoi konferentsii "Susliki Evrazii.* (*Rody Spermophilophis: proiskhozhdeniye, sistematika, ekologiya, povedeniye, sokhraneniye vidovogo raznoobraziya*)" (Proc. Russ. Sci. Conf. "Ground Squirrels of Eurasia. (Spermophilophis Genera: Origin, Taxonomy, Ecology, Behavior, Conservation of Species Diversity)"), 2005, pp. 43–44.
15. Klyuev, N.A., Sleptsov, I.Yu., Gladchenkov, A.A., et al., New cave archaeological sites of Primorye (First Results of Research), *Tr. Inst. Istor. Arkheol. Etnogr. Dal'nevost. Otd. Ross. Akad. Nauk*, 2023, vol. 39, pp. 50–65.
16. Danukalova, G., Tiunov, M., Osipova, E., et al., Holocene palaeoenvironments of southern Sikhote-Alin Mountains (southern Far East), reconstructed from palaeontological data, *Palaeoworld,* 2025, vol. 34, no. 5, p. 200943.
https://doi.org/10.1016/j.palwor.2025.200943
17. Korotkiy, A.M., Features of the development of the natural environment of the Far East in the late Pleistocene–Holocene, in *Rossiiskii Dal'nii Vostok v drevnosti i srednevekov'e: otkrytiya, problemy, gipotezy* (Russian Far East in the Ancient and Medieval Time: Discoveries, Problems, Hypotheses), Vladivostok: Dal'nauka, 2005, pp. 15–58.
18. Evstigneeva, T.A., Bondarenko, O.V., and Utescher, T., Climate and vegetation changes in southern Primorye (Russian Far East) since the Last Glacial Maximum: A quantitative analysis, *Palaeoworld,* 2025, vol. 34, no. 1.
https://doi.org/10.1016/j.palwor.2024.06.009
19. Kolesnikov, B.P., *Rastitel'nost'. Yuzhnaya chast' Dal'nego Vostoka* (The Southern Part of the Far East), Moscow: Nauka, 1969.
20. Korotkiy, A.M., Volkov, V.G., Grebennikova, T.A., et al., Far East, in: Velichko, A.A. and Nechaev, V.P., Eds., Cenozoic climatic and environmental changes in Russia, *Geol. Soc. Am.,* 2005, vol. 382, pp. 121–137.
https://doi.org/10.1130/0-8137-2382-5.121

Publisher's Note. Pleiades Publishing remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.
AI tools may have been used in the translation or editing of this article.