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Historical Biology

An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/ghbi20

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To cite this article: Elena V. Syromyatnikova & Maria S. Tarasova (13 Dec 2024): A racerunner lizard (Lacertidae: *Eremias*) from the Early Pleistocene of Crimea, Historical Biology, DOI: 10.1080/08912963.2024.2439937

To link to this article: https://doi.org/10.1080/08912963.2024.2439937

Published online: 13 Dec 2024.

https://doi.org/10.1080/08912963.2024.2439937

A racerunner lizard (Lacertidae: *Eremias*) from the Early Pleistocene of Crimea

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ABSTRACT

A nearly complete frontal bone of a racerunner lizard (Lacertidae: *Eremias*) is described from the Lower Pleistocene deposits of the Taurida cave – a famous site of fossil vertebrate fauna in Crimea, north Black Sea region. A comparative study of the frontals in the genus *Eremias* by micro-CT highlighted a few diagnostic features and suggested that the *Eremias* from the Taurida cave cannot be attributed to any modern species, including *Eremias arguta*, which inhabited Crimea currently. The specimen from the Taurida cave represents the first Early Pleistocene record of the genus and the oldest European record of the genus to date. Our data suggests that *Eremias* dispersed into Crimea already in the Early Pleistocene, not in the Holocene as was suggested earlier. The past range of *Eremias* in Crimea was wider than today and included midland areas. This record extends the distribution range of *Eremias* during the Pleistocene.

ARTICLE HISTORY
Received 1 October 2024
Accepted 1 December 2024

KEYWORDS
Early Pleistocene; Crimean Peninsula; *Eremias*; Lacertidae

Introduction

Eremias is a widespread genus of small and medium-sizes lacertid lizards with approximately 40 species of almost exclusively Asiatic distribution. These species inhabit steppes and deserts from western Asia to Korea and north-eastern China (Szczerbak 2003). Only two species, which have the widest ranges in the genus, extend into the southeastern Europe: *Eremias arguta* (Pallas, 1773) occurs in the Black Sea region from Romania to Ciscaucasia and Eastern Transcaucasia, while *Eremias velox* (Pallas, 1771) occurs in North Caucasus, Dagestan, and the lower Volga region. Despite the present-day diversity of the genus, its fossil record is poor. The oldest record of *Eremias* comes from the Middle Miocene of Morocco (Beni Mellal locality) (Rage 1976), which agrees with the African origin of the tribe Eremiadini (Arnold 1989). Other Neogene records come exclusively from Asia: the Late Miocene of the Gusiniy Perelet locality (Pavlodar 1A and 2B) in Kazakhstan (Chkhikvadze 1984; Vasilyan et al. 2017) and the Late Pliocene of the Badkhyz locality in Turkmenistan (Ananjeva and Gorelov 1981). Böhme (2007) suggested the possible presence of *Eremias* based on a single bone from the Late Miocene of the Builstyn Khudang locality in Mongolia. Later, Čerňanský and Augé (2019) described and figured new and abundant material from this locality as Eremiadini indet. The younger *Eremias* occurrences are known from the Middle Pleistocene of China (Li et al. 2004) and from the Middle Holocene of Southern Urals (Danukalova et al. 2011) and the Holocene of the Baikal Region (Schepina et al. 2016), both in Russia. The European records of *Eremias* are young, coming from Middle and Late Pleistocene localities: Ozyornoye-1 of Ukraine (Ratnikov and Krokhmal 2003) and Kosika, Elasy, Seroglazovka, and Volnaya Vershina-1 of the European Russia (Ratnikov 2001, 2002; Zastrozhnov et al. 2020, 2021). A possible *Eremias* sp. (or *Lacerta* sp.) was described from the Middle Pleistocene of the Roslavl locality based on a single caudal vertebra (Ratnikov 2002), but an exact generic allocation based on this bone is not possible. Besides, a member of Eremiadini indet. has been described based on several fused frontals from the Late Miocene Monticino Quarry fissure fillings in Italy (Villa et al. 2021).

Here, we describe a frontal bone of *Eremias* found in the Taurida cave of the Crimean Peninsula, which represents the first Early Pleistocene and, so far, the oldest known European record of the genus. This study is part of an ongoing project on fossil vertebrates of the Taurida cave.

Material and methods

The Taurida cave is located near the Zuya Village in the Belogorsk District of the Crimean Peninsula in the north Black Sea region (Lopatin et al. 2019; Figure 1). The cave is a famous Pleistocene vertebrate locality, which has yielded a large number of fossil bone remains. During seven years (2018–2024) of field investigations in the Taurida cave, several dozen mammalian taxa (rodents, shrews, chiropterans, lagomorphs, carnivorans, perissodactyls, artiodactyls, proboscideans) were identified (Lopatin 2019a, 2019b, 2019c, 2021, 2022, 2023a, 2023b; Gimranov et al. 2020, 2021, 2023; Lopatin and Tesakov 2021, 2024, others). The rich bird association includes giant ostrich *Pachystruthio* and new bird taxa, sandgrouse *Pterocles bosporanus* Zelenkov, 2023 and grey partridge *Enkuria voinstvenskyi* Zelenkov, 2024 (Zelenkov et al. 2019; Zelenkov 2022, 2023, 2024). The amphibian assemblage with six taxa (Syromyatnikova and Tarasova 2024) and some selected reptiles (testudinid turtle and viperid snake; Syromyatnikova 2023; Syromyatnikova and Lopatin 2024) have been described recently. Small mammals of the Taurida cave are represented by four associations which correspond to three stratigraphic levels of the Early and Middle Pleistocene age (Lopatin and Tesakov 2024). The bulk of fossil material of the Taurida cave came from the main bone-bearing red layer of the Early Pleistocene age (about 1.8–1.6 Ma) and correlating it to the Late Villafranchian and the MQ1 zone of the European mammal biochronological scale. The *Eremias* frontal bone described here comes from a fossiliferous layer at the depth of ca. 60 cm and is reddish brown, both suggesting

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Published online 13 Dec 2024

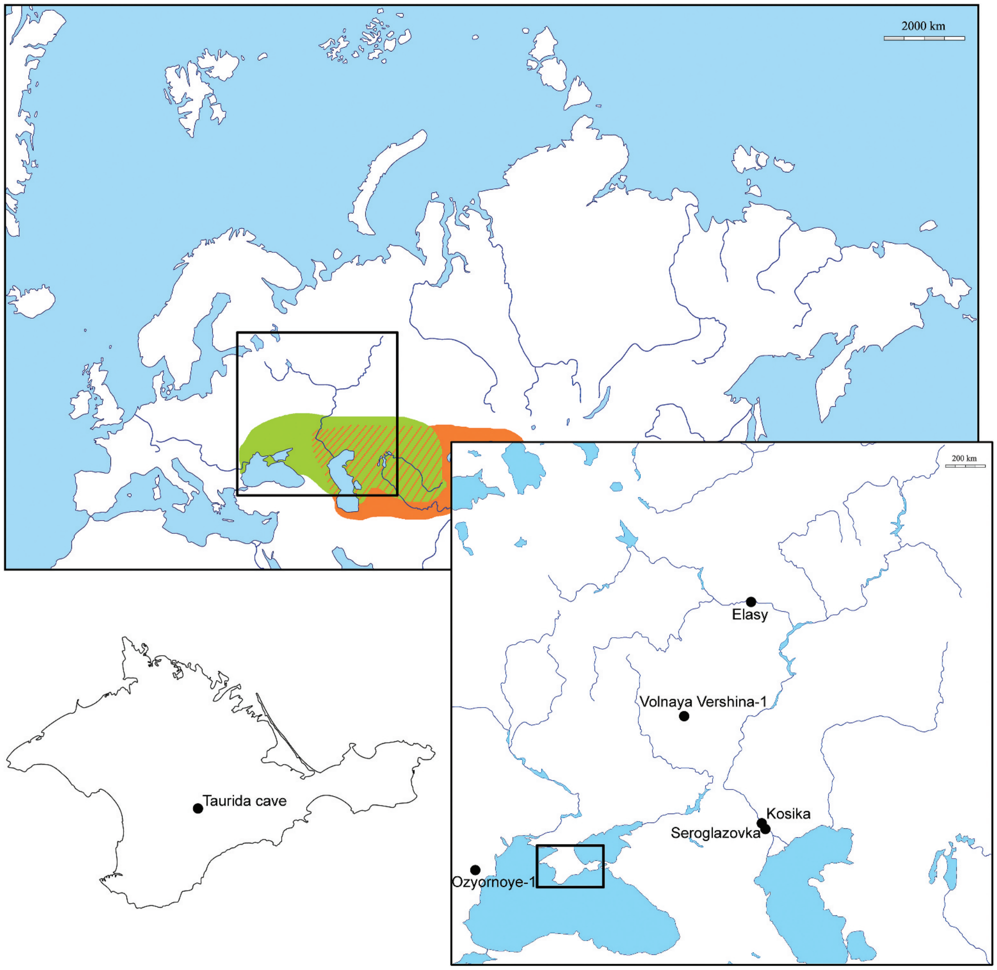

Figure 1. The approximate modern range of *Eremias arguta* (green) and *Eremias velox* (orange)(top), European fossil records of *Eremias* (bottom right) and geographic location of the Taurida cave in the Crimean Peninsula (bottom left).

that it comes from the main bone-bearing layer (Lopatin and Tesakov 2024). Modern skeletons of *Eremias arguta* (Pallas, 1773) (3 specimens, PIN H 120, 122, 123), *Eremias velox* (Pallas, 1771) (3 specimens, PIN H 124–126), *Eremias strauchi* Kessler, 1878 (2 specimens, PIN H 127, 128), *Eremias grammica* (Lichtenstein, 1823) (5 specimens, PIN H 129–133), *Eremias lineolata* (Nikolsky, 1897) (4 specimens, PIN H 134–137), *Eremias multiocellata* Günther, 1872 (2 specimens, PIN H 138, 140), *Eremias persica* Blanford, 1875 (1 specimen, PIN H 145) from the osteological herpetological collection of the Paleontological Institute (PIN H) were used for comparative purpose along with literature data. The fossil and recent specimens studied are housed at Borissiak Paleontological Institute (PIN) of the Russian Academy of Sciences in Moscow, Russia. Light images were obtained on a ZEISS Stemi 508 (Jena, Germany) stereomicroscope. Additionally, in order to visualise external and internal (vascular pattern) structure, the specimens were scanned using a Neoscan N80 (Belgium) X-ray µCT scanner at Borissiak Paleontological Institute; cross-sections were reconstructed using Neoscan software, and 3D models were built with Avizo v.8. Morphological terminology follows Villa and Delfino (2019).

Systematic palaeontology

Squamata Oppel, 1811
Lacertidae Oppel, 1811
Eremiadini Shcherbak, 1975
Eremias Fitzinger, 1843
Eremias sp.
(Figure 2)

Material

One frontal, PIN 5874/90, Taurida cave, Crimean Peninsula; Early Pleistocene.

Description

The frontal is nearly completely preserved. Its dorsal surface is covered by dermal ornamentation. The bone is formed by two fused elements and has a typical hourglass shape with a narrow central and widened anterior and posterior portions. The anterior margin bears clearly marked and deep articulation surfaces with the

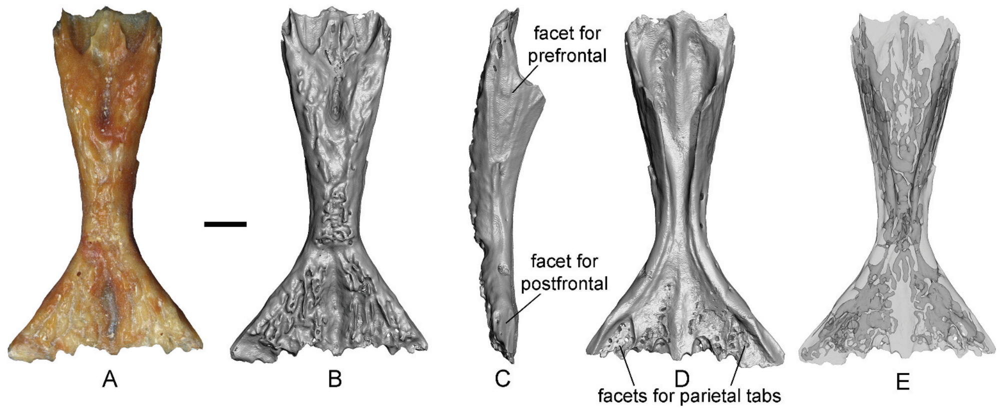

Figure 2. *Eremias* sp., frontal PIN 5874/90, Taurida cave, Crimean Peninsula; Early Pleistocene, in dorsal (A) view; virtual 3D reconstructions in dorsal (B), lateral (C), and ventral (D) views, and 3D model of the vascular mesh (E). Scale bar, 1 mm.

nasals, medially, and smaller and shorter articulation surfaces with the maxilla, laterally (Figure 2(A,B)). The posterior portion is about twice as wide as the anterior one and bears the posterolateral processes directed posterolaterally. The suture with the parietal is interdigitated, partially broken off. Laterally, the bone is slightly curved (Figure 2(C)). Two facets are visible here: an elongated facet for the prefrontal, anteriorly, and a short facet for the postfrontal, posteriorly; both facets are situated distinctly far from each other. The left lateral margin of the bone between these facets is pierced by five large foramina. Ventrally, the frontal cranial crests are well-developed and markedly bent anteroventrally (Figure 2(D)). The anterior processes are broken off. Subtriangular facets for the parietal tabs are clearly marked. The interfacial sulcus is clearly visible at the 3D reconstruction (Figure 2(B)). It is located slightly posteriorly to the mid-orbital constriction. A deep medial groove is visible along the anterior midline part of the bone.

Micro-CT revealed an extensive internal network of interconnected vascular canals and erosion cavities (Figure 2(E)). This network extends over the entire bone except the areas of the facets for the nasals and along the sulcus between the frontoparietal shields.

Remarks

The specimen PIN 5874/90 is assigned to Eremiadini tribe based on a single hourglass-shaped frontal with an interdigitated posterior margin and unfused cranial crests. Geographical situation indicated its affinities rather with *Eremias* lineage than with other members of Eremiadini. The cranial osteology of the modern *Eremias* species has never been studied in detail (see Discussion). Our examination of the species occurring in Europe, i.e. *E. arguta* and *E. velox* (Figure 1), revealed a general similarity in the structure of the frontals between these two species and the specimen described here (Figure 3), i.e. similar proportions, widely diverged posterolateral processes (slightly wider in *E. arguta*), etc. PIN 5874/90 differs from the frontal of the western Asian *E. strauchi* in having a narrower central region and more laterally directed posterolateral processes (Figure 4(A–C)). It differs from the frontals of the above-mentioned species, as well as of *E. grammica*, *E. lineolata*, *E. multiocellata*, and *E. persica*, in being thicker (rather thick in *E. multiocellata*) and its cranial crests being markedly bent anteroventrally (Figure 4(E,H,K,N)). The vascular pattern of PIN 5874/90 differs from *E. arguta* (both adult and young) and *E. velox* in having a more extensive network of canals and cavities (Figure 3(D,H,L)). Based on these observations and taking into account the inadequate knowledge of cranial osteology of the modern *Eremias* species, we assign PIN 5874/90 to *Eremias* sp.

Discussion

The specimen PIN 5874/90 cannot be formally assigned to any modern *Eremias* species extending into Europe (i.e. *E. arguta* and *E. velox*) due to differences in the external and the internal morphology (see Remarks). The internal morphology of reptiles, i.e. the vascular pattern, is currently substantial research area (e.g. Georgalis and Scheyer 2021; Syromyatnikova et al. 2022; Loréal et al. 2023; Čerňanský et al. 2023, 2024). It generally reflects the size and the ontogenetic age of the individual rather than phylogenetic relationships (e.g. de Buffrénil et al. 2008). Indeed, the frontal of an adult modern *E. arguta* (Figure 3(D)) showed a better developed vascular network than that of a young *E. arguta* (Figure 3(H)). However, PIN 5874/90 (Figure 2(E)) differs from the frontals of both *E. arguta*, the adult (whose bone is the same size as PIN 5874/90) as well as the young. The extensive vascular network of PIN 5874/90 suggests the adult age of the individual. Comparing PIN 5874/90 with frontals of all numerous Asian species of *Eremias* was not possible in the current research. However, our preliminary examination of *E. grammica*, *E. lineolata*, *E. multiocellata*, *E. persica*, and *E. strauchi* revealed a rather uniform structure (Figure 4) as well as intraspecific variability in the proportions of *Eremias* frontals. PIN 5874/90 differs from all of the examined modern species by having a thicker frontal. We avoid interpreting the mentioned differences as diagnostic taxonomic characters, but they appear to be informative for further assessing cranial osteology of modern and fossil *Eremias*.

Only a few previous studies focused on the cranial osteology of the modern species of *Eremias*. The first such study was made by Szczerbak (1974), who examined skulls of 10 species but could not find any diagnostic features. Others surveys of the cranial osteology of *Eremias* focused on the *E. multiocellata* species complex (Eremchenko and Panfilov 1999) and the Mongolian *Eremias* spp. (Orlova and Dunaev 1992, 2012). Eremchenko and Panfilov (1999) showed differences in the morphology of some cranial bones between four geographical populations of *E. multiocellata*. The authors compared the same characters in eight species of *Eremias* (including *E. arguta*) and found that a few species differed in the position of the parietal foramen, the presence of pterygoid teeth, and the shape of the septomaxilla. For the frontal bone, a single character, the shape of its anterior margin, was evaluated; however, it showed almost no variation among the examined species. In the analysis of Orlova and Dunaev (2012), individual variations in the proportions of the frontal bone have been mentioned for some

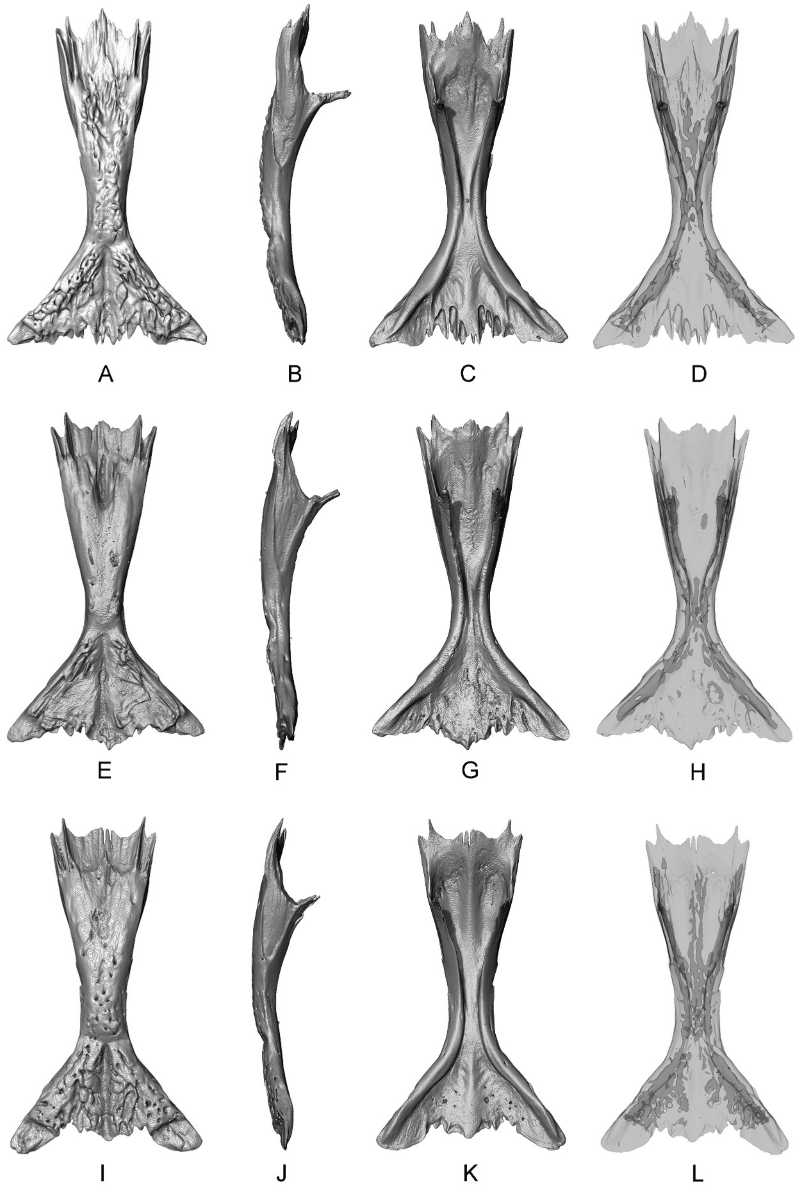

Figure 3. Virtual 3D reconstructions of frontals of modern *Eremias arguta* and *Eremias velox*: (A-D), *E. arguta*, frontal of adult specimen PIN H 120, in dorsal (A), lateral (B), and ventral (C) views, 3D model of the vascular mesh (D); (E-H), *E. arguta*, frontal of young specimen PIN H 122, in dorsal (E), lateral (F), and ventral (G) views, 3D model of the vascular mesh (H); (I-L), *E. velox*, frontal PIN H 124, in dorsal (I), lateral (J), and ventral (K) views, 3D model of the vascular mesh (L). Images not to scale.

Eremias species. Villa and Delfino (2019) described skull osteology of European lizards, but the sample included only a single species of *Eremias* (*E. arguta*). A skull osteology of *Eremias persica* is described by Khosravani et al. (2011) in comparison with the other eremiadine lacertid, *Mesalina watsonana* (Stoliczka, 1872).

The absence of reliable diagnostic osteological characters of the modern species of *Eremias* prevents species-level assignment of fossil remains of this genus. The older Eremiadini records (i.e. Mio-Pliocene) mainly come from the Asiatic (Kazakhstan, Mongolia, Turkmenistan) localities and have been mentioned as *Eremias* sp. (Ananjeva and Gorelov 1981; Chkhikvadze 1984; Vasilyan et al. 2017) or even Eremiadini indet. (Čerňanský and Augé 2019). The younger records, from the Middle – Late Pleistocene, have been determined exclusively based on the geographical distribution of modern species. The European records are mostly represented each by a single vertebra, which, at the current state of knowledge, prevents any specific determination. They have been assigned to *Eremias arguta*, *Eremias* cf. *arguta* or *Eremias* aff. *arguta* (Ratnikov 2001, 2002; Ratnikov and Krokhmal 2003; Zastrozhnov et al. 2020, 2021) and, therefore, should be considered with caution. PIN 5874/90 is the first Early Pleistocene record of the genus and the oldest European record of the genus to date. It supplements the extremely scarce fossil record of *Eremias*, which includes in total only six known European occurrences (Figure 1).

Eremias arguta has the largest distributional range among all species of the genus and is divided into several subspecies, differing from each other in their genetics, body colouration, and proportions. The modern Crimea is inhabited by members of its western subspecies, *E. arguta deserti* (Gmelin, 1789) (Szczerbak 1966). The range of that subspecies extends from the eastern Romania along the Black Sea coast to the southern

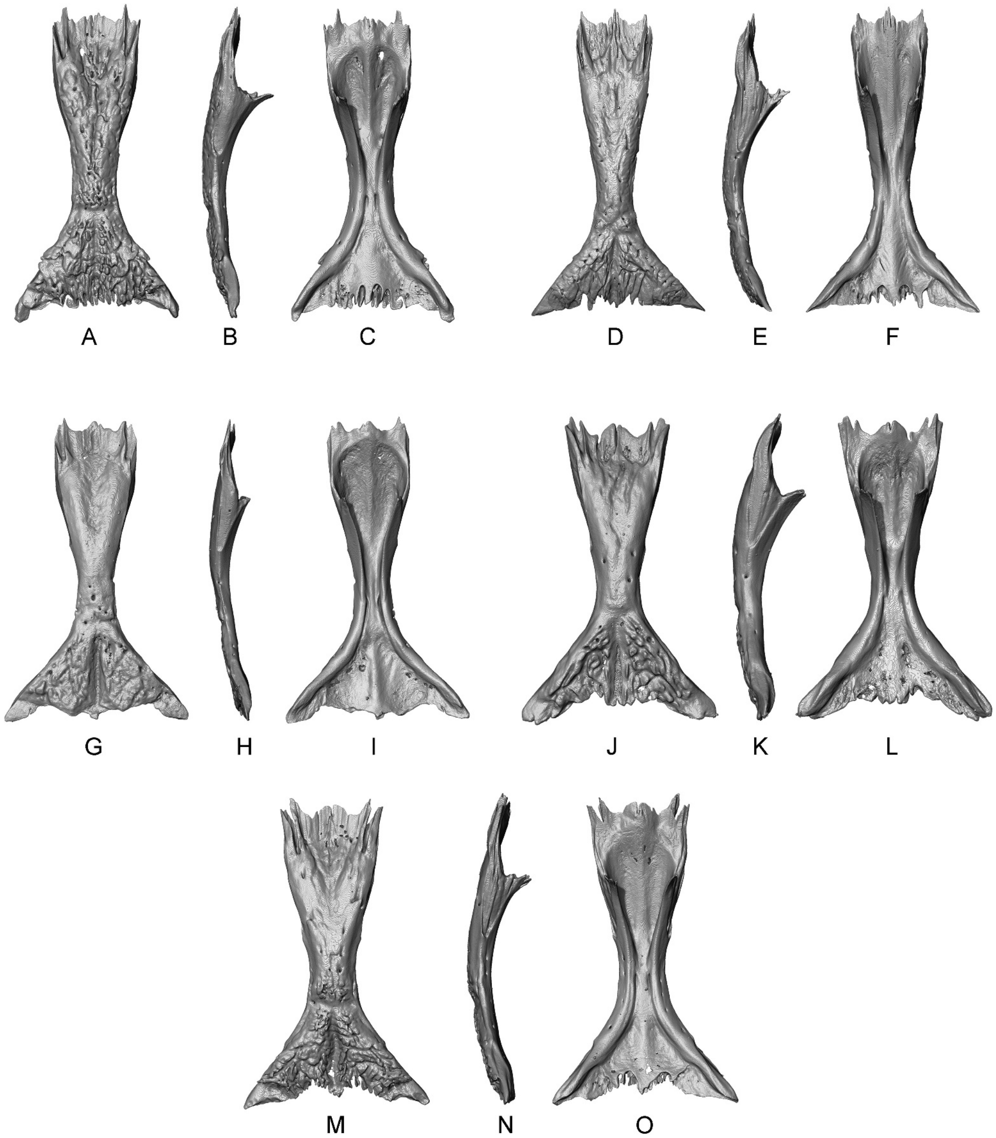

Figure 4. Virtual 3D reconstructions of frontals of selected modern *Eremias* species: (A-C), *E. strauchi* PIN H 127 in dorsal (A), lateral (B), and ventral (C) views; (D-F), *E. grammica* PIN H 129 in dorsal (D), lateral (E), and ventral (F) views; (G-I), *E. lineolata* PIN H 134 in dorsal (G), lateral (H), and ventral (I) views; (J-L), *E. multiocellata* PIN H 138 in dorsal (J), lateral (K), and ventral (L) views; (M-O), *E. persica* PIN H 145 in dorsal (M), lateral (N), and ventral (O) views. Images not to scale.

Ukraine, the Crimean Peninsula and the Ciscaucasia, as well as the northwest coast of the Caspian Sea all the way to the Ural River. In Crimea, *E. a. deserti* is relatively rare, occurs only along a very narrow sea coastal zone in the eastern and western flatland parts of the peninsula, where it is associated exclusively with sand habitats (Szczerbak 1993). The Taurida Cave, where the specimen PIN 5874/90 was found, is located in the central part of the peninsula and rather far from any coastal environments. The new data may suggest that the suitable for this species habitats occurred in the central part of Crimea during the Early Pleistocene or the presence of another *Eremias* species, with different ecological preferences. In any case, the past range of *Eremias* in Crimea was wider than today and included midland areas. Our data suggests that *Eremias* dispersed into Crimea already in the Early Pleistocene, not in the Holocene (Kukushkin 2013). The inconsistency of the Pleistocene and the modern ranges of *Eremias* in Europe was shown by Ratnikov (2001) based on a record of a vertebra of *E. arguta* from the Elasy locality of the Volga River Basin (Republic of Mari El, Russia), which is located north of the modern range of this species (Figure 1).

Acknowledgements

For collecting fossil specimens, we thank A. Lavrov (Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow) and D. Gimranov (Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences, Yekaterinburg). For assistance with microtomography and copy-editing of the manuscript, we thank R. Rakitov (Borissiak Paleontological Institute, Moscow). We are grateful to Andrej Čerňanský (Comenius University in Bratislava, Slovakia) and Hugues-Alexandre Blain (Institut Català de Paleoecologia Humana i Evolució Social in Tarragona, Spain) for the thoughtful review and corrections. The work was supported by the Russian Science Foundation, grant No. 22-14-00214, https://rscf.ru/project/22-14-00214.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The work was supported by the Russian Science Foundation [22-14-00214].

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