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Lagurus lagurus (PALLAS, 1773) and Cricetus cricetus (LINNAEUS, 1758)
(Rodentia, Mammalia) in the Pleistocene of England

[Pp. 111-122; 24 text-figs.]

Lagurus (PALLAS, 1773) i Cricetus cricetus (LINNAEUS, 1758) (Rodentia, Mammalia) w plejstocenie Änglii

Lagurus lagurus (Pallas, 1773) и Cricetus cricetus (Linnaeus, 1758) (Rodentia, Mammalia) в плейстоцене Англии

Abstract: Two species of rodents: Lagurus lagurus (PALLAS) and Cricetus cricetus (L.) were found by the author in the collection from the sediments of Tornewton Cave in Devonshire. They formed part of the fauna of England during the penultimate glaciation and are new to the fossil fauna of Britain. The description of the remains as well as the discussion of their stratigraphic significance is given.

INTRODUCTION

Thanks to long investigations carried out by M. A. C. Hinton (cf. Hinton, 1926) the fauna of fossil rodents of the British Isles is exceptionally well known. It was therefore a great surprise, when in the material of Pleistocene rodents from Tornewton Cave in Devonshire, which I received for study from Dr A. Sutcliffe, Department of Palaeontology, British Museum (Natural History), I found two forms hitherto unknown from the British Isles. Although I examined all the materials of fossil rodents in the possession of the British Museum, I did not find any specimens of these species in the collections from any other of the numerous localities of fossil mammals of that country.

I wish to express my gratitude to Dr A. SUTCLIFFE for allowing me to study this valuable material.

Tornewton Cave, situated in the Torbryan Valley near Denbury in Devon, has recently been investigated by A. J. Sutcliffe and F. E. Zeuner (1962). In their publication they offered a description of the cave and its deposits as well as of the fauna of large mammals. The following survey of the stratigraphy of Tornewton Cave is based on the paper by Sutcliffe and Zeuner, whereas the determinations of rodents are published here for the first time.

The main section of the cave shows a layer of laminated clay devoid of animal remains at the bottom. The laying down of this deposit must have been followed by the formation of stalagmites, which in the form of broken fragments were found in the next layer, called the Glutton Stratum. The Glutton Stratum was an earthy deposit and contained numerous teeth and fragments of bones. Its geological nature indicates frost action, namely, sludging and disturbance typical of periglacial regions. Remains of the following large mammals were found in this layer: Ursus arctos L. (abundant), Canis lupus L. (common), Vulpes vulpes (L.) (common), Panthera spelaea (Goldfuss) (common), Gulo gulo L. (at least two individuals), cf. Coelodonta sp. (rare), Rangifer tarandus (L.) (several specimens), Bos or Bison (rare), Lepus sp. (a few specimens), Meles meles (L.), Cyrnaonyx antiqua (Blainville). The composition of the very abundant fauna of rodents of this layer is presented in Table 1.

The next layer was called the Bear Stratum by Sutcliffe and Zeuner. The nature of this deposit was different from that of the underlying layer. It was stratified, less compact, and showed no traces of sludging. The fauna of large mammals resembled that of the Glutton Stratum, bear remains being still numerous. Rodent fossils were scanty.

The Bear Stratum was overlain by a thin layer of stalagmite. After its formation the cave became a den of hyaenas. The remains of *Crocuta crocuta* (ERXLEBEN) were very numerous and coprolites of this animal also occurred in large quantities. The large mammals were besides represented by *Canis lupus* L., *Vulpes vulpes* (L.), *Panthera spelaea* (GOLDF.), *Ursus* sp., *Dicerorhinus hemitoechus* (FALCONER), *Hippopotamus amphibius* L., *Dama* sp., *Cervus elaphus* L., *Bos* or *Bison* and *Lepus* sp. There were only scanty remains of rodents.

A stalagmite layer covered the Hyaena Stratum. It contained a mineral identified as collophane. The presence of this mineral seems to have been connected with the occurrence of hyaena coprolites.

Inside the cave the layers overlying the Hyaena Stratum had on the whole been destroyed during the previous excavations but they were preserved outside the mouth of the cave. Here, a layer denoted as the Head, in which there were fragments of stalagmite with collophane, was laid down directly on the Hyaena Stratum. This deposit was unstratified and composed mainly of alluvial materials of the valley, disturbed by frost action. It contained reindeer remains.

The Head was directly overlain by a thin layer named the Elk Stratum.

Table 1

Number of specimens of rodents in the strata of the main section of Tornewton Cave

Total	191	2	113	228	6	34	6	19	1660
Micro- mys minu- tus	-		1			1		-	
Micro- Arvico- tus la ter- agrestis restris	হ)	1.	ଚୀ	14	4	14		1	36
Micro- tus agrestis	98		77	123	2	20	9	1	170
Cleth- riono- mys glare- olus	14	-	4	12				က	П
Apode- mus sylva- ticus	258		∞			1	_		-
Micro- tus oeco- nomus			6	19	67			10	1066
Micro- tus nivalis		1	· ·	-	Appare	1	.	4	298
Lem- mus lemmus		1	1			1	. 1		1
Dicro- stonyx torqua- tus		-	1	7	-		- 1		7
Micro- tus gregalis		ì	12	43	1	1			
Lagu- rus lagurus			(1) (1) (1) (1) (1) (1) (1) (1) (1) (1)	-	1.	-	-	-	62
Phodo- pus songo- rus		.1	1	-	İ	1			4
Crice- tus crice- tus			1		1	1.		1	4
	Upper Rodent Layer	Éboulis	Diluvium	Reindeer Stratum	Elk Stratum	Head	Hyaena Stratum	Bear Stratum	Glutton Stratum

Its geological nature was like that of the underlying layer. Remains of the following large mammals were found in this layer: Canis lupus L., Vulpes vulpes (L.), Crocuta crocuta (ERXLEBEN), Ursus sp., Elephas sp., Equus caballus L., Coelodonta antiquitatis (Blumenbach), Cervus elaphus L., Alces sp., Rangifer tarandus (L.), Bos or Bison and Lepus sp.

The next horizon has been named the Reindeer Stratum by Sutcliffe and Zeuner. It was an almost stoneless earthy deposit bearing remains of Canis lupus L., Vulpes vulpes (L.), Crocuta crocuta (Erxleben), Mustela erminea L., Ursus sp., Equus caballus L., Rhinoceros sp., Rangifer tarandus (L.)

(very abundant), Bos or Bison, Talpa europaea L. and Lepus sp.

On top of the Reindeer Stratum, inside the cave, there were some traces of a stalagmite formation, which was overlain by the deposit called the Diluvium by Widger, the first investigator of Tornewton Cave. This layer occurred only within the cave and only its remnants could be examined during the latest excavation. It contained Canis lupus L., Crocuta crocuta (ERXLEBEN), Ursus sp., Bos or Bison and Rangifer tarandus (L.). The Diluvium was probably covered by a stalagmite floor.

Outside the cave the top layers of deposits formed the "Eboulis", which,

like the "Upper Rodent Layer", dated from the Holocene.

The presence of the hippopotamus, red dear, fallow dear and *Rhinoceros hemitoechus*, as well as the geological characters of the deposits, provides evidence of the fact that the Hyaena Stratum was laid down during the last interglacial. Hence the underlying Glutton Stratum must be referred to the penultimate

glaciation (Riss).

The occurrence of the fauna of rodents supports this supposition. Arctic elements (e. g., lemmings) appeared twice in the deposits, but were entirely lacking in the Hyaena Stratum and in the Head, the fauna of which contained forest elements instead. Moreover, whereas the faunas of large mammals were similar in the deposits from the penultimate and last glaciations, the faunas of rodents differed very much. In the Glutton Stratum there were, among other rodents, Cricetus cricetus (L.), Phodopus songorus (Pallas), Lagurus lagurus (Pallas) and Microtus nivalis (Martins). None of these species was represented in the upper arctic layers, where they were replaced by large quantities of Microtus gregalis (Pallas), which, on the other hand, was absent from the lower layers.

Lagurus lagurus (Pallas) occurred in the Glutton Stratum of Tornewton Cave, in which layer it formed 3.8% of the rodent fauna. One specimen was

also found in the overlying Bear Stratum.

Cricetus cricetus (LINNAEUS) was represented in this layer by 2 individuals, i. e., about 0.2% of the fauna of rodents. No specimens were encountered in the other layers of the main section of the cave.

Out of the Main Chamber, numerous remains of small animals were found in a thin layer of deposits in a small chamber called the Vivian Vault. These remains are probably a medley of elements from various periods and contain 1 specimen of Lagurus lagurus and 1 of Cricetus ericetus. The stratigraphy of the Vivian Vault cannot be determined until the rest of the deposit in this part of the cave has been examined.

Lagurus lagurus (PALLAS, 1773)

Material: 3 mandibular fragments with M_1 and M_2 , 4 mandibular fragments with M_1 . Isolated molars: 55 M_1 , 13 M_2 , 8 M_3 , 12 M^1 , 14 M^2 , 26 M^3 ; 4 molar teeth, which are fragmentary or belonged to very young individuals.

Description. The molars are rootless, with no cement in the valleys of enamel. The thickness of enamel is not uniform. Besides the posterior loop, M_1 has 5 enamel triangles. The two anterior ones are as a rule separated from each other, but sometimes may be more or less broadly united, though never as distinctly as in the genus *Pitymys McMurrie*. The anterior loop is similar to that in the group *Microtus arvalis-agrestis*, but its middle part is narrower, rather poorly distinguished from the lateral salient angles. Besides, the shape of the anterior loop shows great variation.

M₂ and M₃ have a characteristic anterior loop, lengthened toward the front and, in addition, 3 closed enamel triangles. Sometimes there are hardly any valleys on the anterior loop and in one specimen this loop is asymmetrical.

M³ is particularly distinctive. It has 3 closed enamel triangles in addition to the anterior loop and a strongly lengthened posterior loop, with more or less well marked lateral salient angles.

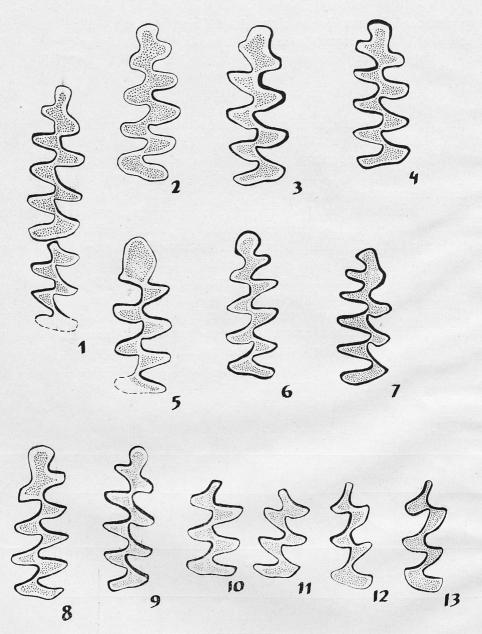
Measurements (in mm)

Mandibular fragments with M_1 — M_2

Number of specimen	1	2	3
$ m M_1\ length$	2.9	2.7	2.6
$ m M_3\ length$	1.8	1.6	1.4

Length of isolated molar teeth

	n	minimum	mean	maximum
M,	38	2.3	2.6	2.9
${ m M_2}$	12	1.4	1.5	1.6
M_3	7	1.4	. 1.7	1.8
\mathbf{M}^{1}	12	1.6	1.9	2.1
\mathbf{M}^2	11	1.6	1.7	1.9
M^3	22	1.8	2.1	2.3

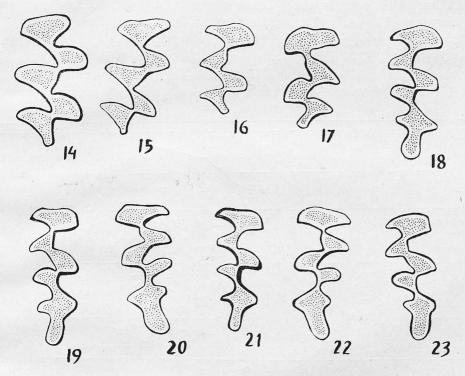


Figs. 1—13. Lagurus from Tornewton Cave. 1 — M_1 — M_2 ; 2—9 — M_1 ; 10—11 — M_2 ; 12—13 — M_3 . Fig. 7 represents a young tooth of *Microtus oeconomus* (drawing made by mistake).

Discussion

The lack of roots and cement in the molars and the shape of the surface of these teeth indicate unambiguously that they represent the species *Lagurus lagurus* (Pallas). The variation of teeth observed in the material from Tornewton Cave coincides with that found in the contemporary members of this

species in so far as it is possible to infer on the basis of the poor comparative material which I have at my disposal and the figures hitherto published, especially those in the book by Ognev (1950). The only character which sometimes occurs in the specimens from Tornewton Cave and which I have never seen in the contemporary material is a tendency towards the fusion of the two anterior enamel triangles on M_1 .



Figs. 14—23. Lagurus lagurus from Tornewton Cave. 14—15 — M^1 ; 16—17 — M^2 ; 18—23 — M_3

There are no data on the measurements of particular teeth of *Lagurus lagurus* in literature. Only Janossy (1964) reports that in 80 M³ of contemporary specimens measured by him the length came to 1·4—2·2 mm, which on the whole agrees with the measurements of the specimens from Tornewton Cave.

The present distribution of Lagurus lagurus (Pallas) in the U. S. S. R. covers the steppe part of eastern Europe, east of the Dniepr and north of the Caucasus and the Caspian Sea, reaching to the Oka on the north. Further east this range includes the southern part of Siberia up to the Aral Sea and Syr Darya in the south (Bobrinskij, Kuznetsov, Kuzjakin, 1965; Gromov et al., 1963). In the territory of the Mongolian People's Republic the range of Lagurus lagurus includes a small area near Ubsa Nor on the north and near the Chinese frontier, south of the Altai Range, in the south-west (Bannikov, 1954). This distribution suggests that Lagurus lagurus occurs also in the north-western part of Chinese Turkestan.

Lagurus lagurus is an inhabitant of steppes and deserts and dwells also in mountainous steppes up to 2200 m a. s. l.

Outside the present range in Asia, fossil remains have been recorded from the caves of the north-western Altai Mts. (Vinogradov, 1922) and from Transbaykalia, where they were found in loess near Troitskosavsk (Ognev, 1950).

In Europe, beyond the present range, fossil remains of *Lagurus lagurus* are known from the caves in the Crimea (Gromov, 1961), from La Adam Cave in Dobruja in Romania (Dumitrescu et al., 1961), and from several fossil localities in Hungary: Subalyuk Cave (Janossy, 1962), Kalman-Labrecht cave (Janossy, 1964), Nagyharsanyhegy 6 (Kretzoi, 1956), and Tata (Janossy, 1960). The Romanian and Hungarian finds date from the last interglacial or the early period of the last glaciation. *Lagurus lagurus* has recently

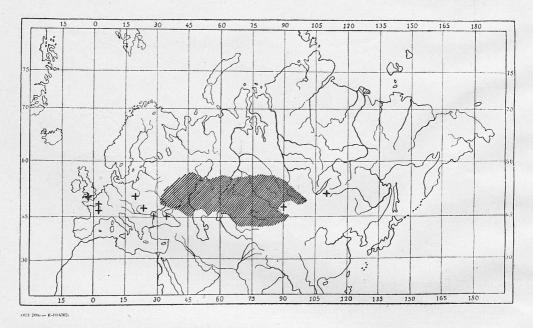


Fig. 24. Distribution of recent and fossil Lagurus lagurus. + fossil localities outside the present range

been recorded also from Fontéchevade, from the fauna of the early Würm glaciation (Chaline, 1965; Chaline, Michaud, 1966) and from two other caves in France: Le Régourdou and La Chaise (Chaline, in litteris). I discovered it in Poland in two caves near Ojców, Żytnia Skała and Mamutowa.

Lagurus lagurus (Pailas) belongs to the well defined group of Microtinae, sometimes denoted by the term Lagurini (Kretzoi, 1955). They show a number of relationships with the genus Dicrostonyx Gloger, which belongs to the lemmings. The Lagurini appeared towards the end of the Pliocene and at the beginning of the Pleistocene, as the earliest voles with molar teeth growing throughout life. In America they were then represented by the genus Plio-

lemmus Hibbard, which had a very elongated M₁ and became extinct without issue. The forms of the Lagurini which lived in Europe and Asia at that time had a straightly shaped M₁ with fused enamel loops (Laguropsis Kretzoi). In the lower Pleistocene they are replaced by the forms included in Lagurodon Kretzoi, in which the two anterior enamel triangles are fused as in the genus Pitymys McMurtrie. The later species exemplify the passage from Lagurodon to Lagurus lagurus (Pallas) in a continuous manner.

At present the genus Lagurus Gloger comprises, besides L. lagurus (Pallas), the well distinguished species L. luteus (Eversmann, 1840), living now only in Mongolia and in the Chinese part of Turkestan, but known from subfossil and fossil remains also farther to the west, up to Romania. The third member of this genus is the American species L. curtatus (Cope, 1868). It shows a number of clear-cut differences in relation to the species of the Old World and is placed in the separate subgenus Lemmiscus Thomas, sometimes raised to the rank of genus.

Cricetus cricetus (LINNAEUS, 1758)

Material. The remains from the Glutton Stratum probably belonged to two specimens. Specimen 1, with almost entirely unworn teeth, is represented by a fragment of the left mandible with M_1 — M_2 , right M_1 , left M^2 and a small fragment of a molar.

Specimen 2, with teeth more worn and somewhat smaller, is represented by a fragment of the left mandible with M_1 — M_3 , a fragment of the right mandible with M_2 — M_3 and a fragment of the maxilla with right M^1 — M^2 .

Upper right M2, slightly worn, was found in the Vivian Vault.

Description. The fragments of the skull and teeth under study do not differ from the corresponding elements of contemporary Cricetus cricetus (L.).

Measurements. Specimen No. 1 (teeth almost unworn): M_1 — M_2 —6.3 mm, M_1 —3.5 mm, M_2 —2.9 mm, M^2 —2.9 mm.

Specimen No. 2 (teeth weakly worn): M_1 — M_3 —8.6 mm, M_1 —3.2 mm, M_2 —2.6 mm, M_3 —2.9 mm; M^1 — M^2 —6.3 mm, M^1 —3.6 mm, M^2 —2.9 mm. Specimen from the Vivian Vault (M^2) is 3.1 mm long.

Discussion

The morphology of the teeth and the size of the specimens from Tornewton Cave indicate that they belong to the species $Cricetus\ ericetus\ (L.)$. This species is also known from the fossil materials of the early Pleistocene of Europe. Schaub (1930) reported the M_1 — M_3 length measured on 77 mandibles from the Late Pleistocene of Hungary to be between 7.6 mm and 9.0 mm, the average being 8.24 mm. According to Miller (1911) the M_1 — M_3 length of contemporary specimens amounts to 7.6—8.2 mm.

At the present time *Cricetus cricetus*, the only member of the genus *Cricetus* Leske, occurs in eastern Europe and in the western part of Asia. In western and central Europe its range is insular in character and seems to be characterized

by gradually increasing expansion. The hamster inhabits a part of France, Belgium, Holland, Germany, and southern and central Poland. Farther to the east its range is more continuous and includes Hungary, part of Romania, and the whole southern and central part of European Russia. In Asia it reaches to western Siberia and the Chinese part of Turkestan. Several, not very distinct, subspecies have been distinguished within this range. In the opinion of Gromov et al. (1963), there is generally a tendency towards the increase of measurements proceeding from the west towards the east and from the north southwards.

Cricetus cricetus occurs in steppes, parklands and meadows. In Europe its occurrence is associated with arable fields.

Forms resembling the contemporary hamster lived as early as the Pliocene. In the Early Pleistocene there were forms varying in size and many of them were given separate names, to which different authors assign a different systematic value. In general, it seems that in the Pleistocene we have to do with one species, whose size changed under the influence of climatic changes. Particularly large forms were derived both from the Early and from the Late Pleistocene (Schaub, 1935).

The only known specimen from Great Britain comes from the Cromer Forest Bed. It is an upper jaw with a toothrow, 9.3 mm long, described by Newton (1909) as *C. cricetus runtonensis*. A characteristic feature of this specimen is the strong development of the anteroexternal cusp on M¹, which evidently protrudes to the outside. The singleness of the specimen makes it impossible to find whether this character is constant or individual.

At any rate, it seems certain that the presence of remains of the hamster in Tornewton Cave provides evidence of its expansion to the British Isles in the Late Pleistocene independenty of the appearance of the same species or a different form in the Early Pleistocene.

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STRESZCZENIE

Autor opracował zbiory gryzoni z osadów Tornewton Cave, położonej blisko Denbury, w Devon w Anglii. Osady tej jaskini wykazują następstwo dwu faun chłodnych, oddzielonych warstwami z fauną cieplejszą, pochodzącą z ostatniego interglacjału. Autor podaje skład fauny gryzoni z poszczególnych warstw Tornewton Cave (tabela 1) oraz zajmuje się szczegółowo szczątkami Lagurus lagurus (Pallas, 1773) i Cricetus cricetus (Linnaeus, 1758), znalezionymi w dolnej warstwie z fauną zimną, pochodzącej prawdopodobnie z okresu przedostatniego zlodowacenia. Lagurus lagurus nie był dotąd znany z Wysp Brytyjskich. Cricetus cricetus znany był z jednego okazu ze starszego plejstocenu z Forest Bed, była to jednak odmienna forma, opisana jako C. c. runto-

nensis Newton, 1909. Obecność obu gatunków dowodzi dalekiej migracji ku zachodowi Europy gatunków związanych z warunkami stepowymi w okresie zlodowacenia Riss.

PESIOME

Автор обработал коллекции грызунов из отложений Торньютон Кэйв, расположенных неподалёку от Денбюри, в Девоне в Англии. Отложения этой пещеры обнаруживают смену двух холодных фаун, разделённых слоями с фауной более тёплого периода, относящейся к последнему межледниковому периоду. Автор даёт состав фауны грызунов из различных слоёв Торньютон Кэйв (таблица 1), а также подробно рассматривает ископаемые остатки Lagurus lagurus (Pallas, 1773) и Cricetus cricetus (Linnaeus, 1758), обнаруженные в нижнем слое с холодной фауной, относящейся, по всей вероятности, к периоду предпоследнего оледенения. Lagurus lagurus до сих пор не обнаруживали на Британских островах. Cricetus cricetus был представлен одним экземпляром из Форест Бэд, однако это была несколько иная форма, описанная как С. с. runtonensis Newton, 1909. Присутствие обоих видов доказывает факт далёкой миграции на запад Европы в период оледенения Рисс степных животных.

Redaktor zeszytu: doc. dr M. Młynarski