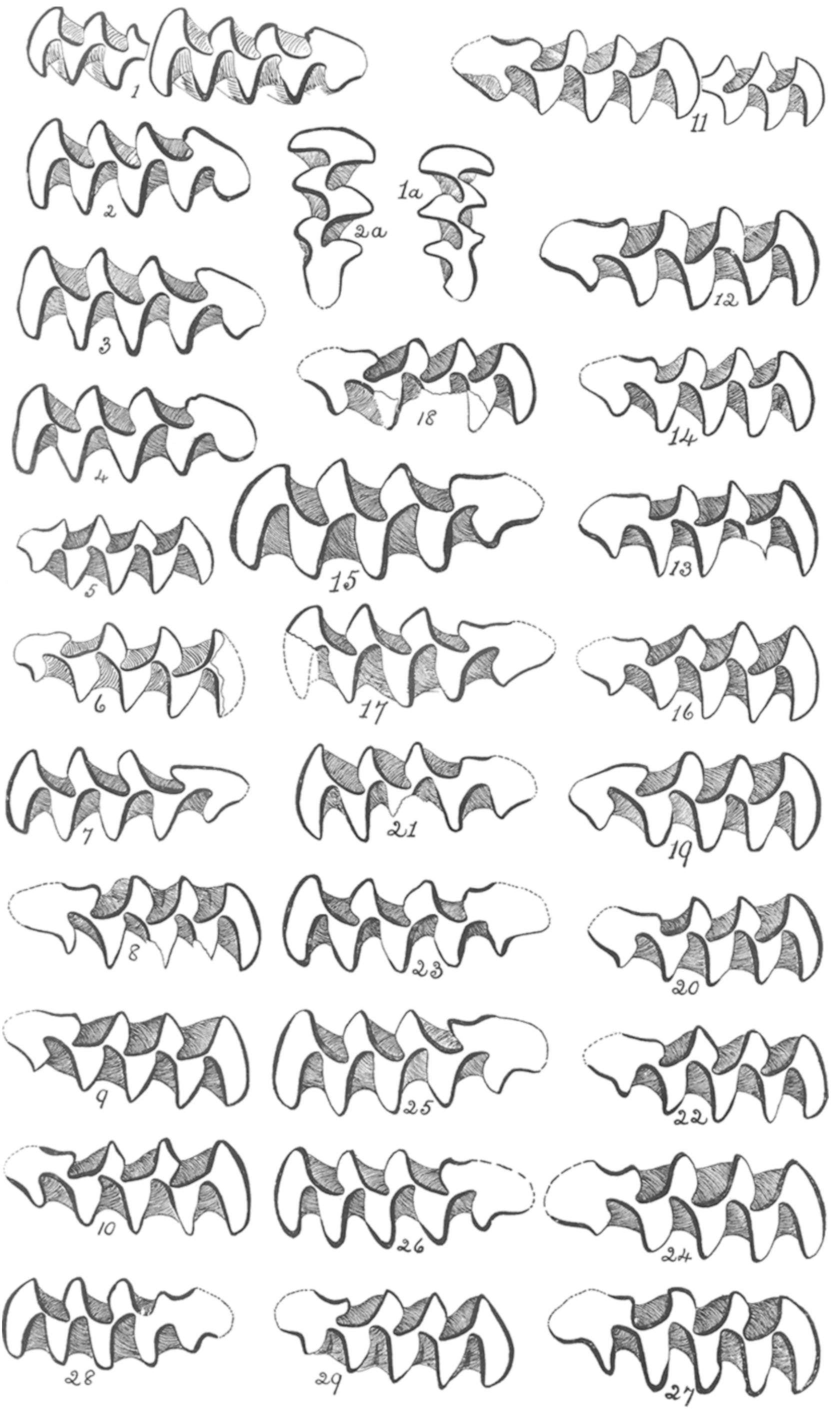

M. A. C. H.

MOLAR TEETH OF *MICROTUS NIVALIS*, ETC.

ON THE EXISTENCE OF THE ALPINE VOLE (*MICROTUS NIVALIS*, MARTINS) IN BRITAIN DURING PLEISTOCENE TIMES.

(Read April 5th, 1907.)

By MARTIN A C. HINTON

[PLATE I.

IN the year 1841, Martins and Bravais discovered a new species of Vole living at a great altitude on the Alps, which Martins subsequently described under the name of *Microtus nivalis.** In 1852, Gerbe published an account of a closely allied animal from the Basses-Alpes which he called *M. leucurus*,† whilst in 1853 Wagner described yet another close ally from the Eastern Alps—*M. petrophilus.*‡ An interesting account of *M. nivalis* and its two allies is given by Blasius.§ None of these forms live to-day, so far as is known, at a smaller elevation than 3,000 feet above the sea. *M. leucurus* and *M. petrophilus* are characteristic of the lower peaks of the outer Alpine regions. *M. nivalis* inhabits the Central Alps, and from being very rare at comparatively low levels it becomes more and more frequent as one ascends, its maximum abundance being reached at or about the snow line. But far above this limit it may be found inhabiting little pinnacles of rock temporarily bared of snow and scantily clothed with the most stunted Alpine vegetation. In such places, says Blasius, it lives not merely through the short Alpine summer but through a hard Alpine winter of nine or ten months duration, secure under a covering of snow. In 1847, De Selys Longchamps‖ showed that this remarkable species also inhabited the Pyrenees. It has since been discovered by Dr. Forsyth Major living on the summit of the Gran Sasso d'Italia, in the Abruzzi, at a height of 2,921 metres, and also in various parts of the Apennines.

It is evident from the remarkable habitat of this species, or rather group of closely allied forms, that all facts relating to its distribution in past times must be of considerable interest to the geologist. We are indebted to Dr. Forsyth Major for our earliest knowledge of *M. nivalis* as a Pleistocene mammal, for in 1873 he recorded its occurrence in the Grotta di Levrange in Lombardy, and in the Grotta di Parignana, near Pisa.¶ He afterwards discovered its fossil remains in the Grotta di Verezzi in Liguria, and in the Grotta della Palmaria in the island of Palmaria, near

* Martins, *Revue de Zool.*, 1842, p. 331; *Ann. d. Sc. Nat.*, 1843, xix, p. 87.
† Gerbe, *Revue de Zool.*, 1852, p. 260.
‡ Wagner, *Münchener Gelehrt. Anzeig.*, 1853, p. 307.
§ Blasius, *Säugethiere Deutschlands*, 1857, p. 359.
‖ De Selys Longchamps, *Revue Zool.*, 1847, October.
¶ Forsyth Major, *Atti. del. Soc. Ital. d. Sc. Nat.*, xv, pp. 375, 378, 389

Spezia. Since then this species has been detected on numerous occasions among the fossil voles of the Continental Pleistocene deposits, as for example, by Dr. Nehring in the caves of the French part of Switzerland, and by Dr. Woldřich in the ossiferous fissures at Zuzlawitz in Bohemia and in Moravia.

Messrs. Blackmore and Alston in 1874* described a lower jaw of a vole from the brickearth of Fisherton, and gave a figure of the first lower molar. This they suggested might be referable to *M. nivalis*, but they hesitated to make a decided reference, as the teeth of *M. ratticeps* from the same deposit varied to such an extent as to render it possible that this example might be an extreme form of the latter species. I have not seen the specimen, but judging from the figure while the pattern of the *m.* $_{\overline{1}}$ is somewhat similar to certain ill-defined forms of *M. nivalis*, yet it is not sufficiently distinctive to be regarded by itself as good evidence of the occurrence of this species at Fisherton.

In 1882, Mr. E. T. Newton† described and figured a lower jaw from the Upper Freshwater Bed at West Runton, in which the anterior loop of the first lower molar is suggestive of some of the forms of *M. nivalis.* Mr. Newton did not record the species as a Forest Bed form, regarding the evidence as too meagre, but in any case all possibility of such a reference is precluded, since, as Dr. Forsyth Major first pointed out to me this jaw, in common with the others figured on Pl. xiv of Mr. Newton's work, does not belong to the subgenus *Microtus*, the *m.* $_{\overline{1}}$ of which possesses five closed triangles, but to *Pitymys*, a subgenus in which the anterior lower molar is composed of a posterior loop followed by three closed triangles, which are followed in turn by an outer and an inner triangle communicating widely with each other and shut off from the anterior loop, completing the tooth in front.

In 1899, Mr. E. T. Newton‡ provisionally referred certain of the lower jaws from the Ightham Fissure to *M. nivalis.* He says: "The front lower cheek tooth of this species is not always to be clearly distinguished from extreme forms of *M. glareolus;* but among the very many examples of the latter species which have been obtained by all the collectors from the Ightham Fissure, there are several which have the inner part of the anterior prism well developed, so that five inner and four outer angles may be counted. It seems highly probable, therefore, that these are the remains of *M. nivalis.*" Six of the specimens so referred to are in the collection of Messrs. Corner and Kennard, and these I have carefully examined. Those which belong to old enough individuals have the teeth distinctly rooted,

* Blackmore and Alston, *Proc. Zool. Soc.*, 1874, p. 466, fig. 2g.
† Newton, E. T., "Vertebrata of Forest Bed." *Mem. Geol. Surv.*, p. 90, Pl. xiv, fig. 7.
‡ E. T. Newton, *Quart. Journ. Geol. Soc.*, lv, p. 425.

and all have the murine incisor root so characteristic of *Evotomys*, and which is quite different in *Microtus*.* Therefore, these remains cannot be referred to *M. nivalis*, but clearly belong to *Evotomys glareolus*.

In 1901, in the report of an excursion of this Association to Grays,† I recorded the occurrence of *M. nivalis* in the brick-earth of that locality. This record was based upon a detached *m.* $_{\overline{1}}$, and a further prolonged study of this tooth has convinced me of the accuracy of this determination. The specimen is again referred to in the sequel, and so far as I know this was the first well-founded record of *M. nivalis* as a former inhabitant of Britain.

The difficulty which obviously exists in determining the remains of this species, arises from the fact that one, in determining the fossil remains of voles, and particularly those obtained from fluviatile deposits, has to rely practically wholly on the evidence afforded by the pattern of the first lower and third upper molars. Now the *m.* $_{\overline{1}}$ of some varieties of *M. nivalis* is occasionally very difficult to distinguish from the extreme forms met with in such species as *Evotomys glareolus*, *M. arvalis*, *M. agrestis* and *M. gregalis*. With regard to the *m.* $^{\underline{3}}$, its typical recent form is usually distinctive enough, but unfortunately this form appears to be very rare in the British deposits.

It is necessary to here allude to one or two points connected with the structure of microtine molars in general, as they throw a good deal of light on certain problems connected with the variations in form seen in the two diagnostic teeth, viz.: the *m.* $_{\overline{1}}$ and the *m.* $^{\underline{3}}$. It has long been known that the investing enamel sheet is not of equal thickness throughout; that in lower molars it is thicker on the anterior walls of the prisms than it is on the posterior ones, and that the converse to this holds good as regards the upper molars.‡ Dr. Forsyth Major has demonstrated the fact that in well-worn teeth the enamel sheet entirely disappears at one point in the anterior loop of the *m.* $_{\overline{1}}$, and also in the posterior loop of the *m.* $^{\underline{3}}$.§ Consequently the comparatively soft dentine here appears as forming part of the periphery of the tooth, and, being no longer constrained by the enamel, runs riot, and most extensive variations of form are the result. Practically all the specific distinctions to be demonstrated in the dentition of the subgenus *Microtus* are drawn from the variable parts of these two teeth, *i.e.*, their terminal loops. The fact that the terminal loops vary so greatly throughout the subgenus is really not so surprising as the equally well-attested fact that on the whole the variations observed very constantly range themselves round certain

* Nehring, *Zeits f. ges. Naturwiss.* Bd. xlv (1878), p. 235.
† Hinton, *Proc. Geol. Assoc.*, xvii, p. 142.
‡ See for example the figures given by Dr. Merriam in *N. Am. Fauna*, No. 2, Pl. iv, etc.
§ Forsyth Major, *Proc. Zool. Soc.*, 1902, vol. i, p. 106, text fig. 15, fig. 27, and in many of the teeth of *Mimomys* there figured.

points, and that these points coincide in general with species, and, in some cases, even with varieties founded often on quite other characters. Dr. Rörig and Dr. Borner, in a recent elaborate paper* enter very exhaustively into the subject of the inequalites of the enamel sheet, evidently thinking themselves the first to observe these features. They say that the enamel becomes a very thin continuous band in the terminal loops of $m._{\overline{1}}$ and $m.^{\underline{3}}$, but this is hardly an accurate statement, for except in very young teeth careful examination will, as a rule, show it to be entirely absent as above stated.

Several authorities, among whom may be mentioned Woldřich, and Rörig and Börner, have asserted that certain series of all but insensible variations may be traced, which lead from one species with a comparatively simple molar pattern, through other species to a form characterized by molars of a more complex type. Although not in a position to discuss this question fully on the present occasion, I wish to briefly allude to it, as it is of importance to the palæontologist. Woldřich's researches were conducted principally on a large series of fossil jaws from the Moravian Caves.† Inspection of his numerous figures will show that not only are some of the variations very discontinuous, but that his arrangement of the series is quite an arbitrary one in many cases, various alternative arrangements being open to us, so that we may proceed to any given point in the series by very different routes. Rörig and Börner ‡ on the other hand have argued that the dental pattern supposed by palæontologists to characterize *M. gregalis* occurs also in the *arvalis* group of species as an individual variation. This, I venture to think, is not a serious objection to the diagnostic value of the molar pattern for two reasons; firstly, because *M. gregalis* is precisely that recent species of which we possess the minimum of knowledge; and secondly, whether the pattern supposed to differentiate its $m._{\overline{1}}$ from all other species occurs in the *arvalis* group or not, there can be no doubt that the great majority of the *arvalis* individuals possess a pattern peculiar to their own group, and different from the pattern of *gregalis*. The general principle that in so far as each group of species possesses a pattern, on the whole peculiar to itself, which is shared by the great majority of its individuals, such patterns are diagnostic of species is, in my opinion, very difficult to assail, although at the same time it is not always safe to record a species upon an isolated tooth, since the diagnostic pattern may occur, though very rarely, in abnormal individuals of other groups.

The $m._{\overline{1}}$ of *M. nivalis* consists essentially of a posterior loop—five more or less completely closed triangles and an anterior loop—these elements being common to this tooth in the whole

* Rörig and Börner, *Arb. a.d. Kais. Biol Anstalt f. Land-und Forstwirthschaft*, 1905, Band v, pp. 37-79.

† Woldřich, *Sitzb. d. k. Akad. Wien, Math. Nat. Cl.*, Bd. 90, p. 387.

‡ Rörig and Börner, *op. cit.*, pp. 71-78.

subgenus *Microtus*. The posterior loop and the closed triangles or prisms afford us no distinctive characters unless it be that the angles terminating the prisms are somewhat sharper than is usual in most other species. In the form called *M. petrophilus* there is a tendency for the hind wall of the prisms, and especially those of the outer side, to become bilobed.* The principal distinction must be drawn, however, from the form and composition of the anterior loop. If we examine this part of the $m._{\overline{1}}$ of *M. nivalis* we find that the outer and inner posterior walls of the anterior loop are formed of thin enamel, and that they correspond to the posterior walls of the fourth outer and fifth inner prisms respectively. From the junction of the inner posterior wall with the inner side of the anterior loop we find a band of very thick enamel extending forwards to near the antero-internal extremity, where it ends off abruptly. This we immediately recognise as the anterior wall of the fifth inner prism turned from the transverse position held by its predecessors into a longitudinal one. Similarly on the outer side we find a stretch of very thick enamel, the anterior wall of the fourth outer prism, but which does not extend so far forwards as its companion of the inner side, though, like the latter, it ends off quite abruptly in front. Between the abrupt terminations of these stretches of thick enamel there is a broad arcuate expanse of dentine, forming the periphery of the triturating surface, and which in the well-worn crown is entirely free from any investiture of enamel (Plate I, Figs. 1, 7, 10, and 18). Thus it is clear that no rudiment of either a sixth inner nor a fifth outer prism enters into the composition of the anterior loop of *M. nivalis*. The fifth inner and the fourth outer prisms, each considered as a whole, are turned obliquely backwards out of the normal lateral position to a greater or less degree—a character which attains its highest expression in the typical *M. nivalis* and in *M. imitator*, Bonhote.† Sometimes only one of the prisms shows this axial revolution. Its tendency is to increase the length of margin formed by dentine alone. The anterior loop may be completely closed behind or pretty widely confluent with the fourth inner prism.

Apart from its rooted condition the $m._{\overline{1}}$ of *Evotomys* distinguishes itself by the fact that the fifth inner angle is usually rudimentary, by the more concentrated and confluent character of the whole tooth, and also by an interesting tendency to bilateral complication of the posterior loop—a variation to be frequently seen in this remarkable genus, but of extremely rare occurrence in *Microtus*. The possession of five closed triangles by the $m._{\overline{1}}$ of *M. nivalis* at once, of course, distinguishes this tooth from any of the subgenera, *Pedomys*, *Pitymys*, *Arvicola*, etc.

* Blasius, *Säugethiere Deutschlands*, p. 360, fig. 196. The figure shows this feature on the second inner prism of $m.\overline{2}$.

† Bonhote, *Ann. & Mag. Nat. Hist.*, Ser. 7, vol. xv, pp. 197-199.

The species from which it is necessary to carefully distinguish *nivalis* are *M. ratticeps*, *M. arvalis*, *M. agrestis*, *M. gregalis*, etc. In the $m._{\overline{1}}$ of *M. ratticeps* the fourth inner prism is widely confluent with the anterior loop; the fourth outer is very feebly developed and usually only present in a flattened-out condition forming an enamel wall to the anterior loop. The fifth inner shows no backward turning, and there may be a small sixth inner prism.

The $m._{\overline{1}}$ of the typical *M. arvalis* distinguishes itself at once by the fact that the fifth inner and fourth outer prism if not shut off are yet quite distinct from the anterior loop, and do not help to form it. There is often a sixth inner and a fifth outer prism. In some varieties the fifth inner tends to merge with the anterior loop, but there is no backward turning and consequently the anterior loop is very different in form to that of *M. nivalis*. Sometimes the fourth outer prism shows a backward turning, but this usually results in more distinctly separating the prism from the anterior loop. Certainly nothing is seen either in *M. arvalis* or in its near ally, *M. agrestis*, which ever approaches the typical *M. nivalis*, *M. leucurus*, or *M. petrophilus*, and such forms as do come near some of the ill-defined teeth of *M. nivalis* show on examination either an extra prism in front or some difference in form which satisfactorily serves to distinguish them.

The group of voles in which the distinction of the $m._{\overline{1}}$ from that of *M. nivalis* presents the greatest difficulty is undoubtedly that which may be regarded as represented by *M. gregalis*. And here the difficulty is felt, not when dealing with the typical forms, for they are distinct enough, but when dealing with some of the ill-defined teeth occasionally met with, especially in the *M. leucurus* and to a less degree in the *M. petrophilus* sections of the *M. nivalis* group.

The typical $m._{\overline{1}}$ of *M. gregalis* distinguishes itself from this tooth in other groups by some very characteristic features. The third outer infold or cement space is wide and to a lateral view quite open. The result of this is that its anterior wall passes into the anterior loop without forming a backwardly projecting angle and usually without forming a fourth outer angle at all. The external border of the anterior loop is much elongated and approximately straight; this is well seen in the figures given by Woldřich,* Newton,† and others. On its inner side the anterior loop develops one or two angular projections, thus giving rise to a fifth or even a sixth inner angle; and this fifth inner angle never shows the backward turning so frequently seen in *M. nivalis*. In addition, the thick parts of the enamel are usually appreciably thinner than in *M. nivalis*. The long,

* Woldřich, *Sitzb. d. k. Akad. Wien, Math. Nat. Cl.*, Bd. lxxxii, Abt. ii, Taf. ii, fig. 12, Bd. lxxxiv, Abt. i, Taf. ii, fig. 48.

† Newton, *Quart. Journ. Geol. Soc.*, vol. l, Pl. xi, fig. 12a.

straight anterior loop is well seen even in the "arvaloid" form of Dr. Woldřich* where a fourth outer angle is developed. I have examined at one time or another a great number of fossil jaws referred to the *M. gregalis* group, and as far as my experience goes the variation is principally confined to the development or absence of a small sixth inner angle, the degree of openness of the third outer infold which varies within quite narrow limits, and the extent to which the long, straight outer wall of the anterior loop tends to become curved or broken up into small angular waves.

It is now necessary to detail the evidence upon which my determination of the *M. nivalis* group as a constituent of the British Pleistocene fauna is based. The remains yielded by the deposits of the Lower Thames Valley will be first noticed, and afterwards those from other localities will be dealt with.

All the nivaloid remains so far known from the Thames deposits have been obtained from the brickearths of the Middle Terrace. There is no trace of *M. nivalis* among the few vole remains known from the High Terrace deposits, but little or nothing can be based on this because not only are fossiliferous sections in these deposits exceedingly scarce but Dr. Forsyth Major† has already shown that a nivaloid vole occurs in the far older Upper Freshwater Bed of West Runton, so that we may conclude that the *nivalis* group first established itself in Britain in late Pliocene times.

Grays Thurrock.

As already mentioned, I recorded the occurrence of *M. nivalis* in the Grays brickearth in 1901. The record rests on a right *m.* $_1$ possessing a short anterior loop with a somewhat angulated antero-internal extremity, thus resembling the recent *M. petrophilus* (Pl. I, fig. 5). Comparison with Dr. Forsyth Major's figure will show that the specimen stands about midway between *M. nivaloides* of the West Runton deposit and *M. petrophilus.*

Crayford and Erith.

The brickearth of Crayford and Erith has yielded remains referable to the *M. nivalis* group in abundance, associated with such other voles as *M. ratticeps*, *gregalis*, and at least two members of the *gregalis* group which are new to science, *Arvicola amphibius*, and the Lemmings. Numerous examples are contained in the collections of Mr. A. S. Kennard, Mr. G. White, and myself, and I daresay others occur in several Crayford collections which I have not yet examined. Mr. White's specimens were obtained from the great Crayford pit, while Mr. Kennard collected from the new pit to the north of this. My best thanks are due to both

* Woldřich, *op. cit.*, Bd. lxxxiv, Ab. i, Taf. ii, fig. 47.
† Forsyth Major, *Proc. Zool. Soc.*, 1902, vol. i, p. 106, text fig. 15, fig. 19.

these gentlemen for the kindness with which they placed their collections at my disposal.

One of the most characteristic examples I have seen is a right $m._{\overline{1}}$ in Mr. White's series (Pl. I, fig. 6). The short arrow-head-shaped anterior loop is very similar to some of the recent examples from Italy, kindly lent to me by Dr. Forsyth Major while the slightly angulated antero-internal extremity of the loop resembles what is seen in *M. petrophilus*. A left $m._{\overline{1}}$ in Mr. White's collection affords a very good illustration of another type of *M. nivalis*, characterised by a rather long-pointed anterior loop, the fourth outer and fifth inner prisms being turned backwards (Pl. I, fig. 7). This tooth is very much like the form figured by Rörig and Börner (*op. cit.*, fig. 44*d*). A right $m._{\overline{1}}$ in my collection shows a somewhat similar form, in which the anterior loop is very long, and the thick enamel on the outer side—*i.e.*, the anterior wall of the fourth outer prism preserves some of its primitive concavity—a character which allies the specimen with a well-marked form or species of the *nivalis* group, which will be described later on (Pl. I, fig. 8).

A right $m._{\overline{1}}$ in Mr. White's collection (Pl. I, fig. 9) shows a *M. leucurus*-like form, the fourth outer prism not being produced backwards into a prominent angle. A very fine right $m._{\overline{1}}$ in Mr. Kennard's collection shows pronounced backward revolution of the fourth outer and fifth inner prisms, and, moreover, admirably illustrates the parts which the thick enamel walls and bare dentine play in the structure of the anterior loop (Pl. I, fig. 10).

The anterior half of a right ramus in Mr. White's collection contains the $m._{\overline{1}}$ and $m._{\overline{2}}$ (Pl. I, fig. 11). The former tooth is interesting, recalling as it does in some respects the $m._{\overline{1}}$ of the Kashmir species, *M. imitator*, recently described by Mr. Bonhote. The $m._{\overline{2}}$ of this specimen has the anterior prisms confluent with each other.

An imperfect right ramus presented to the Museum of Practical Geology, by Mr. Kennard, contains the $m._{\overline{1}}$ (Pl. I, fig. 12); the form of the anterior loop approaches the Clevedon species to be described later. It remains to notice some specimens from Crayford which approach *M. leucurus* in form.* These have a wide open third outer infold, not unlike that of *M. gregalis*, and the fourth inner prism is more or less confluent with the anterior loop, as in *M. ratticeps*, but the thick enamel of the outer side, *i.e.*, the anterior wall of the fourth prism and the structure of the inner side of the loop, satisfactorily distinguish these teeth from the $m._{\overline{1}}$ of either of the species mentioned. I have drawn two of these specimens, one belonging to Mr. White and one to Mr. Kennard (Pl. I, figs. 13 and 14). One

* *Cf.* Woldřich, *Sitzb. d. k. Akad. Wien, Math-nat Cl.*, Bd. lxxxiv, Abt. i, Taf. ii, fig. 28.

(fig. 14) is interesting, as showing a little thin enamel following the thick stretch on the inner side, the tooth having belonged to a young individual.

WICKHAM.

In the Spurrell collection (Museum of Practical Geology, No. 5649) the anterior half of a left ramus containing the $m._{\overline{1}}$ is preserved. The specimen is of very large size, and I have had some difficulty in making up my mind as to its affinities. The form and structure of the anterior loop probably indicate a species of the *nivalis* group (Pl. I, fig. 15). The enamel is very thick, aud I believe the jaw to belong to a form distinct from any of those hitherto noticed, but which in some respects approached *M. leucurus* and in others *M. malei*—the new species which is described later from the Clevedon cave. I have preferred, however, to wait for further material before bestowing a new name upon this jaw.

With regard to the deposits other than those of the Thames I have so far made a detailed search for the Alpine vole in the collections from two localities only, viz., the Ightham Fissure and the cave near Clevedon, in Somersetshire, which has lately been investigated by Dr. Male, his brother, and Prof. Reynolds. As regards the Ightham Fissure there is, so far as I have yet been able to ascertain, no evidence of the presence of *M. nivalis* there, and this fact, as I shall endeavour to show in the sequel, goes far to prove the late Pleistocene age of that deposit.

CLEVEDON CAVE.

Dr. H. C. Male very generously presented me with a small series of the numerous jaws of *Microtus* which he found in the Clevedon deposit. After a very careful examination of this material I came to the conclusion that a large vole belonging to the *nivalis* group was represented among the cave fossils. On my informing Dr. Male of my opinion he kindly placed the remainder of the collection in my hands for investigation. Mr. E. T. Newton had previously examined this series, and had sorted the specimens out into the *M. ratticeps*, *M. gregalis*, and *M. nivalis*-like forms, and I should state here that in the shortness of the time which I had at my disposal to devote to this large series Mr. Newton's work was of the greatest value to me, because it enabled me to go direct to the points upon which I required evidence. To both Dr. Male and Mr. Newton I would here tender my warmest thanks.

The nivaloid voles from Clevedon may be divided into two series, viz., those referable to existing members of the group, and those in my opinion belonging to a distinct and hitherto unknown form, (*a*) Jaws indistinguishable from recent forms of the *M. nivalis* group.

The first specimen to be noticed is the anterior portion of a right ramus containing the $m._{\overline{1}}$ and $m._{\overline{2}}$ and the incisor. The pattern of the $m._{\overline{1}}$ (Pl. I, fig. 16), is very distinctive of *M. nivalis*, and as regards the anterior loop is intermediate in form between the teeth shown in fig. 44*d* and *c* of Rörig and Börner (*op. cit.*). With regard to the $m._{\overline{2}}$, the second outer infold does not meet the enamel wall of the opposite side, but on the other hand more nearly does so than is usual in recent *M. nivalis*. However, there is a good deal of variation among recent individuals in this respect. Another very fragmentary right ramus containing the $m._{\overline{1}}$ supplies us with similar evidence. Unfortunately, three of the inner prisms are badly mutilated, but the anterior loop is intact. This (Pl I, fig. 18), agrees perfectly with one of the forms figured by Rörig and Börner (fig. 44, *d*, *op. cit.*), and can only be referred to *M. nivalis*. The presence of a *petrophilus*-like form at Clevedon is shown by a fragment of a right ramus containing the $m._{\overline{1}}$ and $m._{\overline{2}}$, the former with the characteristic short anterior loop (Pl. I, fig. 19). The *M. leucurus*-like form which we have already seen to occur at Crayford, is also represented among the Clevedon forms. Two rami, a right and a left, each containing the $m._{\overline{1}}$ and $m._{\overline{2}}$, and each, unfortunately, wanting the hinder part, are certainly referable to this form. The $m._{\overline{1}}$, though differing in slight details in each specimen, exhibits a structure very similar to that of the Crayford specimens (Pl. I, figs. 20-21). The $m._{\overline{2}}$ is as in normal *Microtus*, *i.e.*, the second outer infold advances far enough across the crown to substantially shut off the two anterior prisms from each other. Other examples referable to one or other of the nivaloid forms are seen in figs. 17 and 22.

(*b*). Nivaloid jaws not referable to existing members of the *M. nivalis* group.

We now have to consider a series of jaws which, although referable to a large member of the *nivalis* group, present certain features which appear to be sufficiently distinctive to justify a separate specific designation. I have made very careful drawings of a representative set of the first lower molars of this series (Pl. I, figs. 23-29). Inspection of these drawings will show that the $m._{\overline{1}}$ of this form distinguishes itself from that of the other members of the *nivalis* group; firstly, by the greater or less development of the antero-internal extremity of the anterior loop, so as occasionally to form a slight sixth inner angulation; secondly, the thick enamel of the outer wall of the anterior loop, *i.e.*, the anterior wall of the fourth outer prism retains the concavity which characterises the anterior walls of normal prisms, and this feature, of course, enhances the apparent projection of the fourth outer angle. With these modifications of structure the anterior loop of the $m._{1}$ of the Clevedon species usually combines great breadth. For this new form I venture to propose the name of *M. malei*, in order to associate it with the gentleman to whom I am indebted for the material enabling me to define it.

It is of interest to notice that *M. malei* is represented in the deposits of the Thames Basin. Thus Dr. Forsyth Major showed me the $m._{1}$ of a vole from Wickham in the British Museum which appeared to be indistinguishable from the Clevedon species, while in Mr. White's collection from Crayford there is a right $m._{1}$ which only differs from the Clevedon specimens in the somewhat slighter depth of the fourth inner infold or cement space (Pl. I, fig. 29). Some of the examples in Mr. Kennard's collection, also, as already mentioned, approach this form.

THE SKULL AND $m.^{3}$.

The skull in the *M. nivalis* group, as is well known, presents certain aberrant characters which, taken in conjunction with the dentition, strongly mark the group off from the other sections of the subgenus *Microtus*. It is therefore to be regretted that hitherto no example from British deposits has been preserved. This is a desideratum which the caves and fissures of Somersetshire will probably supply.

With regard to the $m.^{3}$ this tooth in recent *M. nivalis* usually possesses a pattern of three inner and three outer angles (Pl. I, fig. 2a). I have so far looked in vain for a last upper molar of this type among the British specimens. Very few maxillary teeth were preserved from the Clevedon Cave, so that the specimens before me from that locality may belong to some of the other species of *Microtus* which occurred in the cavern. Numerous examples are before me from Crayford, and of these some, I think must belong to *M. nivalis*. Yet they all differ from the usual recent form in having the internal corner of the posterior loop angulated so that there are four inner angles instead of three. The $m.^{3}$ of a young skull of recent *M. nivalis* from Monte Cimone in the collection of Dr. Forsyth Major possesses the rudiment of such a fourth inner angle (Pl. I, fig. 1a), and this seems to suggest that the fourth inner angle is a disappearing structure in the *M. nivalis* group, since it may have been permanently developed in the adult *M. nivalis* of Pleistocene England but now is only met with in the young individuals. In the eastern part of the range of the group, *i.e.*, in Kashmir, a nivaloid vole, *M. imitator*, Bonhote, occurs which possesses a last upper molar of still more complicated form than that which may have characterised the $m.^{3}$ of our Pleistocene races, since this tooth has four outer as well as four inner angles.*

* Bonhote, *Ann. & Mag. Nat. Hist.* Ser. 7, vol. xv, p. 198.

MEASUREMENTS OF THE JAWS CONTAINING THE TEETH FIGURED IN PLATE I.

Specimen.	1	2	3	4	Specimen.	1	2	3	4
Monte Cimone, fig. 1	4.75	3.03	2.6	3.99	Clevedon Cave, fig. 22	4.11	3.74	2.98	4.82
Monte Cimone, fig. 2	3 91	3.4	2.9	4.8	Clevedon Cave, fig. 19	3.4	3.18	3.09	4.92
Crayford, fig. 14	3.68	3.58	2.91	—	Clevedon Cave, fig. 23	6.08	4.14	3.31	4.92
Crayford, fig. 11	4.28	3.52	2.79	4.28	Clevedon Cave, fig. 24	4.76	4.33	3.22	4.82
Crayford, fig. 12	4.52	3.76	3.3	—	Clevedon Cave, fig. 25	4.48	—	3.1	5.1
					Clevedon Cave fig. 26	5.68	3.94	2.98	4.76
Clevedon Cave, fig. 16	4.28	—	3.07	4.96	Clevedon Cave, fig. 27	5.05	4.6	3.17	5.27
Clevedon Cave, fig. 17	4.63	4.14	2.61	3.84	Clevedon Cave, fig. 28	4.15	4.07	2.9	4.53
Clevedon Cave, fig. 18	4.25	4.3	2.97	—					
Clevedon Cave, fig. 20	3.84	3.7	2.22	4.33					
Clevedon Cave, fig. 21	3.48	4.14	2 91	4.38	Wickham, fig. 15	4 9	—	3.73	4.97

(1) Length of diasteme.
(2) Height of ramus at fourth inner prism of $m._1$.
(3) Length of $m._1$ (alveolar).
(4) Length of $m._1$ and $m._2$ along alveolar border, inner side.
The measurements are in millimetres and were made with the camera lucida and 5 inch objective.

Conclusion.

In my opinion the evidence that has been detailed in this paper renders it practically certain that the *M. nivalis* group of voles was strongly represented in Britain during Pleistocene times, and we have therefore to consider what bearing this fact has on our ideas of Pleistocene history. Examining the present distribution of this group of voles, one finds that all the existing forms are creatures inhabiting high altitudes, and that as a general rule we may say that the greater the altitude the more abundant is *M. nivalis*. It seems thus to be a group incapable of flourishing far from the vicinity of perpetual snow, and therefore we may argue that at the time it so abundantly peopled certain localities of England those neighbourhoods must have suffered a climate much more severe than that obtaining at the present day. Yet I believe that this conclusion, sound as it may superficially look, is really a false one, and that we only arrive at it by reasoning from premises unnaturally limited. In order to obtain an accurate notion of the story which this or any other group of animals has to tell the geologist we must take into consideration not only the facts relating to the habits and distribution of its living members but all the facts relating to its past history, and to the histories of its former and present contemporaries which we may be able to acquire. In other words, the wider the scope of our premises the more accurate will our deductions tend to become.

It is first necessary to examine, with some care, the earliest microtine fauna of Britain. In the Norwich Crag we meet with the earliest English voles, here represented only by that remarkable genus *Mimomys*, whose history, first outlined by Mr. Newton in 1882,* has since been admirably investigated by Dr. Forsyth Major.† The teeth found in the Norwich Crag are plainly, for the most part, not contemporary with that deposit, but have been derived from some older bed, which, so far as our knowledge goes, is now totally destroyed. The principal species found in the Norwich Crag occurs also in the Pliocene deposits of the Val d'Arno. The voles of the genus *Mimomys*, are characterized by rooted molars, and the $m._{\overline{1}}$ is a tooth which, originally possessing three outer infolds or cement spaces, suffers a progressive atrophy of the third or anterior one. It is a general rule, that the atrophy of any valley intersecting a molar tooth proceeds by a gradual growing or knitting together of its enamel walls, and consequently, as the tooth is worn down, internal portions of the valley or cement space become isolated from external portions and form little detached enamel rings or fossettes on the worn triturating surface, which thus serve to mark the former extent of the valley. Continued wear finally obliterates these enamel rings and then no trace of the former valley can be seen. In species which stand near the starting point of the valley degeneration such internal enamel rings may penetrate the crown to a great depth, and consequently they will persist through a very long portion of the life of the tooth. In the Norwich Crag species, *M. pliocænicus*, this is the case, as is shown by Dr. Forsyth Major.

Coming now to a still later point in Pliocene time, that marked by the East Runton deposit, we find that *Mimomys* still alone represents the voles. Its $m._{\overline{1}}$, however, has degenerated a little further, for the enamel islet tends to disappear at an earlier stage of wear, while, on the other hand, the development of roots is a little more tardy.

In the still later Upper Freshwater Bed of West Runton we meet with *Mimomys*, but now the enamel islet is only found in young teeth. Here, too, the genera *Evotomys* and *Microtus* make their first appearance in England. Two sub-genera of *Microtus* are represented, viz., true *Microtus* and *Pitymys*, most of the remains found belonging to the latter.

* Newton, "Vertebrata of the Forest Bed," p. 83.
† Forsyth Major, *Proc. Zool. Soc.* (1902), vol. i, pp. 102-107.

Whence came these voles? We may infer from the fact that *Mimomys* occurs in the Italian Pliocene that it came from the south, and it seems probable that the other three sections had their original home in Central or South-Central Asia, and that they spread eastwards and westwards so as in later times to acquire a more or less circumpolar distribution, reaching America by North-Eastern Asia, and Western Europe by Asia Minor and Southern Europe. *Pitymys* is especially a good instance in support of this claim for a southern origin, for to-day, driven back from its more northern outposts, it finds a refuge in the home of its immediate ancestors, viz., in Southern Europe. Among the few representatives of true *Microtus* from the West Runton deposits, we find the earliest English member of the *nivalis* group—*M. nivaloides*, Major. The *nivalis* group is essentially a southern one, ranging as it does from Kashmir to the Pyrenees, not occurring north of the Alps, and although in Pleistocene times its range extended as far west as Somersetshire, it appears at no time to have gone farther north than Norfolk or Southern Germany. The point I wish to make on these facts is that we do not owe our late Pliocene or early Pleistocene microtine fauna to the Siberian migration at all, as Dr. Scharff suggests,* but that they came to England from Southern Europe long prior to the arrival of the Siberian forms.

Between the deposition of the Forest Bed series and that of the High Terrace drift of the Thames an enormous interval of time must have elapsed—a gap unspanned by any English mammaliferous deposit, unless, indeed, certain of the cave deposits, such as those containing remains of *Machairodus*, are to be referred to this age. The fauna of the High Terrace drift, so far as it is known, has a good deal of affinity with the Forest Bed series. The voles represented are *Mimomys*, which was detected some years ago by Mr. White and myself,† and *Evotomys*. The *Trogontherium* has been determined by Mr. Newton, and it is noteworthy that the Red-deer which occurs is a small form, being accompanied by a large form of Fallow-deer. This fauna I hope shortly to fully describe, but it suffices to say now that it does not show the mixture of northern and southern forms so characteristic of the later Pleistocene deposits, and which has been so hard to explain.

Of the later Pleistocene deposits the most important series for our purpose is undoubtedly that formed by the Middle Terrace drift of the Thames, for from no other horizon have we obtained so complete and varied a picture of the Pleistocene mammalian fauna. And here at last we meet with evidence of the invasion of England by swarms of mammals which can only have come from Siberia and Eastern Europe. To this invasion must be ascribed

* Scharff, "History of the European Fauna," p. 201.
† Hinton and White, *Proc. Geol. Assoc.*, vol. xvii, p. 414.

the presence of the Lemmings, the numerous species of the subgenus *Microtus*, such as *ratticeps*, *arvalis*, *agrestis*, and the great group of *gregaloid* voles, the genera *Cricetus*, *Spermophilus*, and *Lagomys* among the Rodentia, and of the barren-ground Reindeer, and *Saiga* Antelope among the Herbivora. Some of the older forms, such as *Mimomys*, *Trogontherium*, and the large Fallow-deer had at this stage apparently entirely disappeared, but many others, *e.g.*, the *nivalis* group, continued to flourish.

This brief statement of facts will suffice for the moment, and it is necessary now to examine the question of the climatic conditions of Pliocene and Pleistocene England. The mammalian fauna of the late Pliocene deposits, and that of the High Terrace deposits teach us that during the periods which they represent the climate of Britain must have been a genial one. It is not until late Pleistocene times that the mammaliferous deposits begin to give us contradictory evidence on this point. Here, as we have seen, we first meet with those northern and eastern forms in such numbers as to lead one to postulate cold conditions in order to account for their existence in this country. At the outset it must be admitted that if we have regard only to the present distribution of these cold-forms, if, for example, we take the occurrence of the Arctic Lemming, and recognise that to-day it is confined to high northern latitudes, and that it almost studiously avoids even the scanty shelter of the dwarf birches, which extend far beyond the northern tree limit into the southern parts of its distributional area, it requires no strong effort of the imagination to conjure up the former existence in Britain of Arctic Tundra and sub-Arctic Steppes. And in Germany and Austria, where such evidence becomes still more striking, we, in taking stock of these facts only from the recent habitat standpoint, are almost compelled to adopt such views as those so ably advocated by Prof. Nehring,* Dr. Woldřich† and others. But, unfortunately for the Steppe and Tundra theory, so far at least as Britain is concerned, there exists a large body of undeniable evidence in the other scale, and the acceptation of the theory, moreover, would be in direct conflict with what we now know to have been the actual physical geography of Britain in late Pleistocene times.

Side by side with these new Steppe-forms there flourished in the south of England the old group of southern forms. No doubt, as to day, the different mammals chose places suitable to their different modes of life—those species which preferred the woodland would seek it, and those who disliked it would inhabit the barer uplands. Indeed, as I hope to show on another occasion, we have actual evidence of this selection of localities in the Thames deposits. The cold, which at first sight appears to be

* Nehring, *Ueber Tundren und Steppen*, Berlin, 1890.

† Woldřich. *Mitth. d. Wiener Anthrop. Ges.*, Bd. xi., p. 183, and papers already cited.

necessary to the existence of the Arctic Lemming, would render the existence of the Hippopotamus and Ape impossible, and yet we know that all three animals, and many others having requirements similar to the one or the other type, managed to exist at one and the same time in Southern England. Temperature, we have been often told, is the principal factor governing the distribution of mammals, and it may be conceded that in some cases it is so. The assertion is certainly true, universally, to the extent that an Arctic mammal can no more endure the torrid zone than a torrid mammal a boreal clime. But at the same time one must recognise numerous other factors, as for example, food supply (which probably is the *only* universal governing factor), or the distribution of disease. And when, as in the present case, we are endeavouring to write the history of a remote time where the evidence given by the species which were then living, *qua* temperature, is of so contradictory a nature, pointing, as it does, to two diametrically opposed extremes, surely the right inference is that the temperature cannot have been extreme at all, but that the winters must have been mild to suit the southern forms, and the summers cool in order to accommodate the northern species. To my mind, therefore, the real problem to be solved is not as to what climatic conditions held sway in Britain during the joint tenancy of the northern and southern mammalia, but the question as to what it was that, at a later time, drove some forms northwards, others southwards, and still others to the mountain tops.

In this paper we are concerned only with the voles, but in substance the argument is applicable to the other Pleistocene mammalia. Briefly put my contention amounts to this: that in order to explain the differences in distribution which have been effected since Pleistocene times it is not necessary to invoke any substantial change in climate, and that on the other hand all such differences can be satisfactorily accounted for by taking into consideration the reaction, if I may borrow from the chemist, of one species or group of species on another. The most severe competitor in the struggle for existence that any given species can have is another species of similar organisation performing a similar function in the economy of nature. This principle, notwithstanding some apparent exceptions, is probably universally true. The slightest advantage tells, and the species wanting it is driven back step by step to its original home or local centre of dispersion.

Let us apply this principle to the voles. We have seen that in probably early Pliocene times the north-west of Europe was colonised by a southern group, *Mimomys*, retaining some very primitive features. This group was, so far as we know, the sole representative of the voles living here until we arrive at the stage represented by the Upper Freshwater Bed of West Runton. Towards the end of the Pliocene period new colonists, *Evotomys*, *Pitymys*, represented by several species, and *Microtus*, including the *nivalis* group, arrived, also coming from the south. The date at which *Pitymys* died out in this country has yet to be ascertained. *Mimomys* and *Evotomys* certainly managed to survive here until the time represented by the High Terrace of the Thames. It may also be presumed that some of the forms of true *Microtus*, including the *nivalis* group, similarly survived, for although we have not found their remains in the very few known repositories of the High Terrace fauna, yet we know that the *nivalis* group was abundantly represented in Britain at a still later period, viz., that of the Middle Terrace. Now until this later stage is reached we have no evidence at all of the existence of any group of vole in Britain other than those mentioned above. In the Middle Terrace deposits we meet with the first evidence of the arrival of the Siberian voles. As on the Continent so here, they appear to have swarmed in rapidly. Instead of the two or three species which at this time remained to us as the wreck of the Pliocene microtine fauna, we received perhaps a dozen new forms. This in itself must have considerably increased the severity of the struggle for existence, a struggle which had been previously keen enough, for the Siberian forms on their arrival were confronted, apparently, only by the *nivalis* group, then at its zenith in point of range and variety, and an old and weak member of the *Evotomys* genus.

The outcome of this invasion was that the new-comers completely supplanted the old southern forms. This is one of my reasons for regarding the Ightham Fissure deposit as of late Pleistocene age, for examining the microtine element of its fauna we find no trace of either the *nivalis* group or the older form of *Evotomys*. They have entirely died out, and in their place we find a rich assemblage of the later immigrants. But with the extermination of the British *nivalis* group the reaction of one species on another did not cease. *Arvicola amphibius* alone did not have to strive hard to maintain its position, for it had no rival in function—it had taken the place of the long vanished *Mimomys*, and there was no other microtine to dispute possession. Of the numerous species of true *Microtus* (of which we have still a very imperfect knowledge) and the Lemmings which came in with the Siberian migration, *M. agrestis* alone has managed to survive to our days as a British resident, and *Evotomys glareolus*, so far as England is concerned, has completely ousted its northern rival *E. rutilus*, which I believe to be represented with it in the Ightham Fissure.

Much the same sort of history can be read from the Continental deposits with this difference, that as we proceed eastwards and southwards the less decisive becomes the result of the struggle. This is what we should expect since we are proceeding towards the centres of dispersion, and so we are really overtaking the vanquished forms in the course of their retreat.

The last and most difficult question with which we have to deal is one that may really concern the origin of Alpine and Arctic faunas. The key to the solution of the problem of why the *nivalis* group chose to inhabit the Alpine peaks and should now show such an extraordinary love for the snow line lies, in my opinion, in the geological history of the group. We have seen how this group spread westwards from its original home in the south-east, reaching North-western Europe in late Pliocene times, and how it formerly extended northwards across the plains from the Alps and Pyrenees to the southern and south-western shores of the Pleistocene Sea of Europe. I submit that it is established as a fact that at the time of this great Pleistocene extension of the group the climate was as mild as at present, and probably even more equable, owing to the different distribution of land and water which then obtained. It follows, therefore, that the *nivalis* group is primarily one with a temperate habitat, and consequently its present peculiar Alpine habitat must be regarded as a subsequently acquired attribute.

We have also seen that the *nivalis* group was exterminated in Britain and the plains of Central Europe by the competition of the rival groups of voles which came from the north and east, and that to-day the group has made a last stand in the mountains, where for the moment it appears to be secure enough. On the lower slopes of these mountain regions it might possibly hold its own against the newcomers, and in summer doubtless the conditions of existence would be congenial to the species. But the severe and early frosts of the lower mountain slopes would hardly fail to be detrimental to such a mammal. It would learn from experience that security from the frost could only be had from an early covering of snow, and consequently it would eventually colonise the summits where the snow-fall is early and remains unmelted for nine or ten months in the year. This view of the case is, in my opinion, borne out by a perusal of Blasius's graphic description* of the habits of the species and by examining its known vertical range. Briefly put, these facts go to show that the protection from the frost afforded by the snow is necessary to

* Blasius, *Säugethiere Deutschlands*, 1857, p. 364. As this book is not one of the most accessible in England, it may be as well to quote the paragraph. He says: "Es ist mir kein Beispiel bekannt, dass sie in den Alpen regelmässig unter 3,000 Fuss Meereshöhe gefunden wäre. Auch bei 4,000 Fuss scheint sie in der Regel noch nicht häufig vorzukommen. Von hieraus aber findet man sie in allen Höhen bis zu den letzten Grenzpunkten der Vegetation. In der Nähe der Schneegrenze erscheint sie am häufigsten. Aber sogar über die Schneegrenze geht sie hinaus und bewohnt noch die kleinsten Vegetationsinseln, die mit den kümmerlichsten Alpenpflanzen spärlich bewachsenen Blössen auf der Südseite der hohen Alpenspitzen, mitten zwischen ewigen Schneefeldern, wo die warmen Sonnenstrahlen oft kaum zwei bis drei Monate lang die wöchentlich sich erneuenden Schneedecken überwinden, und die Erde auf wenige Schritte hin frei legen können. In dieser grossartigen Gebirgseinsamkeit verlebt sie aber nicht bloss einen schönen kurzen Alpensommer; sondern unter einer unverwüstlichen Schneedecke begraben einen neun bis zehn Monate langen harten Alpenwinter. Denn sie wandert nicht, obwohl sie sich im Winter Röhren unter dem Schnee anlegt, um Pflanzenwurzeln zu finden, wenn die gesammelten Wintervorräthe nicht ausreichen. Kein anderes Säugethier begleitet die Schneemaus dauernd über die Welt des Lebendigen hinaus bis zu diesen luftigen starren Alpenhöhen; nur einzeln folgt vorübergehend, als unerbittlicher Feind, ein Wiesel oder Hermelin ihren Spuren."

the prosperity of the species in its present elevated home. The conclusion I would draw, therefore, is a paradox, viz, that *M. nivalis* seeks the eternal snows for warmth, and the principle which has been urged here will, I believe, be found to apply to a great number of other mammals which to-day are confined to Arctic and Alpine regions, but which, nevertheless, had formerly a wide range throughout temperate Europe, and that it applies to many members of the Alpine and Arctic flora has been often demonstrated.*

The laws which I have endeavoured to illustrate in these conclusions have, of course, long been known, but curiously they have often been overlooked when dealing with the fossil mammalia. A more general recognition of such principles will lead, in my humble opinion, to the adoption of far sounder and safer views with regard to Pleistocene history than many of those put forward in the past, will do away with the necessity of invoking vast changes in climate to account for the differences existing between the past and present distribution of animals and plants, and may, moreover, have a not unimportant bearing on that nightmare—the extreme Glacial theory.

In conclusion, I have to express my best thanks to Dr. C. I. Forsyth Major, F.Z.S., for the very generous way in which he helped me through my difficulties, to Dr. C. W. Andrews, F.R.S., Dr. Frank Corner, F.G.S., Dr. F. L. Kitchen, F.G.S., Professor S. H. Reynolds, M.A., F.G.S., and Mr. B. B. Woodward, F.G.S., for many acts of kindness. Lastly, I wish to thank Mr. E. T. Newton, F.R.S., for the kindness which I have so often experienced from him. To him we are all indebted as the pioneer of this branch of palæontology in this country, and to his efforts we owe, primarily, the preservation of the material necessary to these researches.

P.S.—Since correcting the proofs of this paper I have had an opportunity of glancing through Dr. Scharff's new book, "European Animals." Dr. Scharff, I think, comes to much the same conclusion as I do, viz., that the Alpine habitat is a secondary one, and I would refer the reader to pp. 54 and 56, and Chapters vii, viii and ix.

EXPLANATION OF PLATE I.

In the figures the black line represents the enamel as seen on the triturating surface of the molar crown, the broken or thin line in the anterior loop represents the region where the enamel is absent, and the shaded areas show the extent of the cement in the valleys of the tooth. The drawings are enlarged to nearly 12 diameters, and were made with an Abbé Camera-lucida.

Fig. 1.—*Microtus nivalis* (recent), Monte Cimone, Modenese Apennines. Anterior mandibular molars, left side; 1 a., $m.^2$ left side. (In collection of Dr. Forsyth Major.)

* Scharff, "History of European Fauna," pp. 78, 79, 161–164, and Bulman, *Natural Science*, vol. iii, 1893.

Fig. 2.—*M. nivalis* (recent), summit of Monte Cimone, $m._{1}$ left side ; 2 a, $m.^{2}$ right side. (In collection of Dr. Forsyth Major.)

Fig. 3.—*M. nivalis* (recent), Monte Vecchio. Apennines of Reggio—Emilia left $m._{1}$ (In collection of Dr. Forsyth Major.)

Fig. 4.—*M. nivalis* (recent ♂), Boscolungo, Pistojese Apennines, left $m._{1}$. (In collection of Dr. Forsyth Major.)

Fig. 5.—*M. nivalis*, Pleistocene, Gray's Thurrock, right $m._{1}$.

Fig. 6.—*M. nivalis*, Pleistocene, Crayford, right $m._{1}$. (In collection of Mr. G. White.)

Fig. 7.—*M. nivalis*, Pleistocene, Crayford, left $m._{1}$. (In collection of Mr. G. White.)

Fig. 8.—*M. nivalis*, Pleistocene, Crayford, right $m._{1}$.

Fig. 9.—*M. nivalis*, Pleistocene, Crayford, right $m._{1}$. (In collection of Mr. G. White.)

Fig. 10.—*M. nivalis*, Pleistocene, Crayford, right $m._{1}$. (In collection of Mr. A. S. Kennard.)

Fig. 11.—*M. nivalis*, Pleistocene, Crayford. The anterior molars of an imperfect right ramus in the collection of Mr. G. White.

Fig. 12.—*M. nivalis*, Pleistocene, Crayford. The $m._{1}$ of a right ramus. (Kennard collection, Museum of Practical Geology, No. 6018.)

Fig. 13.—*M. nivalis*, Pleistocene, Crayford, right $m._{1}$. (In collection of Mr. A. S. Kennard.)

Fig. 14.—*M. nivalis*, Pleistocene, Crayford. The $m._{1}$ of an imperfect right ramus in collection of Mr. G. White.

Fig. 15.—*Microtus*, a species of the *nivalis* group. Pleistocene, Wickham. The $m._{1}$ of an imperfect right ramus.* (Spurrell collection, Museum of Practical Geology (No. 5649.)

Fig. 16.—*M. nivalis*, Clevedon Cave. The $m._{1}$ of an imperfect right ramus in collection of Dr. H. C. Male.

Fig. 17.—*M. nivalis*, Clevedon Cave. The $m._{1}$ of a right ramus in collection of Dr. Male †

Fig. 18.—*M. nivalis*, Clevedon Cave. The $m._{1}$ of a right ramus in collection of Dr. Male.

Fig. 19.—*M. nivalis*, Clevedon Cave. The $m._{1}$ of a right ramus in collection of Dr. Male.

Fig. 20.—*M. nivalis*, Clevedon Cave. The $m._{1}$ of a right ramus in collection of Dr. Male.

Fig. 21.—*M. nivalis*, Clevedon Cave. The $m._{1}$ of a left ramus in collection of Dr. Male.

Fig. 22.—*M. nivalis*, Clevedon Cave. The $m._{1}$ of a right ramus in collection of Dr. Male.

Fig. 23.—*Microtus*, a species of the *nivalis* group, Clevedon Cave. The $m._{1}$ of an imperfect left ramus in collection of Dr. Male.

Fig. 24.—*M. malei*, n sp., Clevedon Cave. The $m._{1}$ of a right ramus collected by Dr. Male.

Fig. 25.—*M. malei*, Clevedon Cave. The $m._{1}$ of a left ramus collected by Dr. Male.

Fig. 26.—*M. malei*, Clevedon Cave. The $m._{1}$ of a left ramus collected by Dr. Male.

Fig. 27.—*M. malei*, Clevedon Cave. The $m._{1}$ of a right ramus in collection of Dr. Male.

Fig. 28.—*Microtus*, sp., Clevedon Cave The $m._{1}$ of a left ramus in collection of Dr. Male. Inserted in the Plate by an error.

Fig. 29.—*M. malei* (?), Pleistocene, Crayford. Right $m._{1}$ in collection of Mr. G. White.

* The thick enamel of the outer side of the anterior loop is shown as extending a little too far forwards.

† The fourth outer angle is made a little too sharp.