UTRECHT MICROPALEONTOLOGICAL BULLETINS

SPECIAL PUBLICATION

A. A. BOSMA

RODENT BIOSTRATIGRAPHY OF THE EOCENE-OLIGOCENE TRANSITIONAL STRATA OF THE ISLE OF WIGHT

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by

ANNEKE A. BOSMA

Aan mijn moeder

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18 tables, 38 text-figures, 7 plates

ABSTRACT

The Paleogene deposits of the Isle of Wight in the Hampshire Basin have yielded mammalian remains at various levels. The lowest level is situated near the base of the Lower Headon Beds, while the highest level is situated in the Lower Hamstead Beds.

The rodent species belonging to the families Pseudosciuridae, Theridomyidae, Cricetidae, Castoridae and Paramyidae are described in detail. One of these, the theridomyid species *Isoptychus headonensis,* is new. The pseudosciurid species *Paradelomys quercyi* is subdivided into two subspecies, *P. quercyi quercyi* and *P. quercyi vectisensis* n. subsp. The taxonomic value of the genera *Paradelomys* and *Isoptychus* is reassessed.

A biozonation is inferred from the sequence of rodent associations. The following zones are recognized from below upwards: *Isoptychus headonensis* Zone, *Paradelomys quercyi vectisensis* Zone, *Paradelomys quercyi quercyi-Suevosciurus palustris* Zone, *Paradelomys quercyi quercyi-Suevosciurus fraasi* Zone, *Ectropomys exiguus* Zone and *Eucricetodon atavus* Zone.

The Headonian is proposed as a new stage in the chronostratigraphic scale of continental deposits. Correlation of the Headonian with the Priabonian and Lower Tongrian of the marine chronostratigraphic stage succession is suggested.

Chapter 1

INTRODUCTION

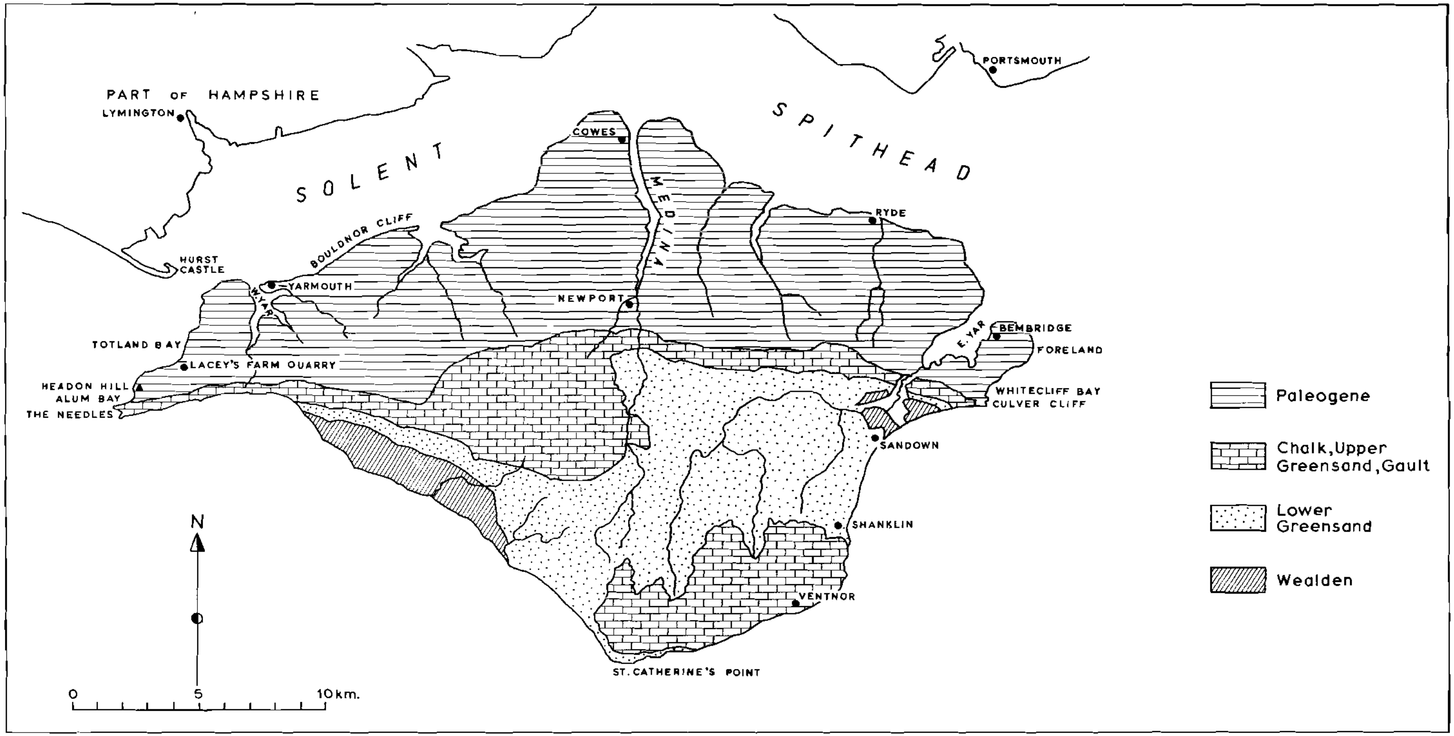
The Rodentia are but poorly represented in the Hampshire deposits, but lower jaws have been assigned to the extinct continental genus Theridomys (R.L. Lydekker, 1900).

The Paleogene deposits of the London and Hampshire Basins represent the western part of the so-called Anglo-Paris-Belgian Basin. Today's exposures of the Hampshire Basin are found in a triangular-shaped area extending over the counties of Hampshire, Dorset, Sussex and the Isle of Wight. Our collecting has been done in the northern part of the Isle of Wight, which is for the larger part composed of Paleogene rocks (text-fig. 1). These rocks rest unconformably on the Chalk.

The exposed strata of the Isle of Wight display a flexure, the central limb of which has an E – W strike across the centre of the island. The topographic expression of this structure is dominated by the axial ridge of vertical Chalk strata. South of this ridge the eroded near-horizontal anticlinal limb shows Cretaceous strata down to the Wealden. In the northern synclinal limb the older Paleogene sediments are turned up vertically against the Chalk ridge, whereas the younger Paleogene sediments show a low angle dip to the north with faint anticlinal and synclinal waves. The Paleogene deposits are mainly exposed in sea-cliffs and in some inland quarries.

The Paleogene succession of the Isle of Wight is essentially composed of clays and sands. Its lower part mainly consists of marine deposits, the top part of which is named the Barton Beds. The marine deposits pass upwards into continental deposits with a few marine intercalations: the Headon, Osborne, Bembridge and Hamstead Beds. This part of the succession is usually interpreted to indicate "an area of lagoons and freshwater lakes, opening into estuaries and arms of the contracting sea, the sea occasionally encroaching over the area" (Chatwin, 1960).

In Europe Late Eocene and Early Oligocene mammalian faunas have usually been collected from localities that have no clear mutual lithostrati-


PART OF HAMPSHIRE
LYMINGTON
PORTSMOUTH
SOLENT
SPITHEAD
COWES
MEDINA
RYDE
BOULDNOR CLIFF
HURST CASTLE
YARMOUTH
W. YAR
NEWPORT
E. YAR
BEMBRIDGE
FORELAND
TOTLAND BAY
LACEY'S FARM QUARRY
HEADON HILL
ALUM BAY
THE NEEDLES
WHITECLIFF BAY
CULVER CLIFF
SANDOWN
SHANKLIN
VENTNOR
ST. CATHERINE'S POINT
N
0
5
10 km.
Paleogene
Chalk, Upper Greensand, Gault
Lower Greensand
Wealden

graphic relations. The presence of stratified continental deposits with fossil remains at various levels on the Isle of Wight, on the other hand, offers possibilities to define biozones in the Late Eocene-Early Oligocene interval.

This paper deals with the Rodentia from cliff-sections at Headon Hill, Totland Bay and Whitecliff Bay. It moreover includes a large number of rodent teeth from Bouldnor Cliff, collected by Mr. R. L. E. Ford (Yarmouth, Isle of Wight), and the Theridomyidae from Lacey's Farm Quarry (University of Bristol site no. 6911; see Bosma and Insole, 1972).

The larger part of the Utrecht material has been collected during a four-weeks campaign in August/September 1970. Testing-samples and supplementary samples have been taken in September 1969 and February 1971 respectively.

Rodent faunas include species of the Pseudosciuridae, Theridomyidae, Cricetidae, Castoridae, Paramyidae and Gliridae. The Gliridae will be the subject of a separate paper.

Chapter 2

METHODS

2.1. Sampling methods.

All the material has been collected by wet sieving of sediment on a set of screens, the finest of which has a 0.5 mm mesh. The sediment of Whitecliff Bay 2A has been treated with acetic acid before sieving, in order to isolate the fossil remains. All residues have been treated with acetic acid before sorting them out.

The amounts of sediment processed are as follows: Headon Hill 1 – 1600 kg; Headon Hill 2 – 1600 kg; Headon Hill 3 – 700 kg; Headon Hill 4 – 300 kg; Headon Hill A – 100 kg; Headon Hill B – 60 kg; Headon Hill C – 300 kg; Headon Hill 5 – 30 kg; Headon Hill 6 – 80 kg; Headon Hill 7 – 400 kg; Totland Bay – 1500 kg; Whitecliff Bay 1 – 1200 kg; Whitecliff Bay 2A – 20 kg; Whitecliff Bay 2B – 300 kg.

2.2. Measuring methods.

The length and width of the isolated cheek teeth have been measured as is shown in text-fig. 3. The length and width of the cheek teeth in jaw fragments have been measured in the same way, unless stated otherwise. Measurements have been taken with a Leitz Ortholux measuring microscope (ocular 10x, objective 3.8x) or a Leitz Orthoplan measuring microscope (ocular 8x, objective 4x), both with mechanical stage and measuring clocks. They are given in 0.1 mm units and are rounded to one decimal place. Owing to a variation in the orientation of the teeth, the measuring error may be larger than 0.05 (= 0.005 mm).

2.3. Statistical analysis.

For elaborate description of the statistical procedures used, the reader is referred to the textbook of Dixon and Massey (1969):

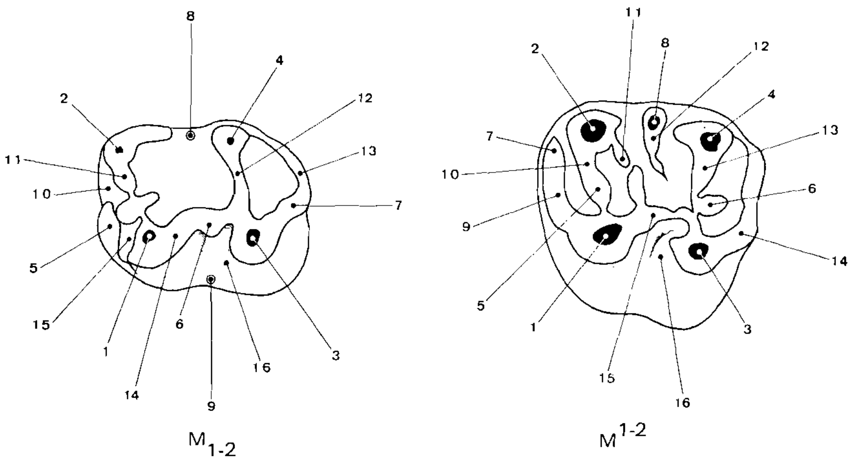
confidence interval: chapter 6–3
F test: chapter 8–2
t test: chapter 8–4
χ^2 test for independence: chapter 13–3
rank-sum test: chapter 17-4

In applying the F, t, χ^2 and rank-sum tests the 5 per cent level of significance has been chosen. Confidence intervals have been constructed with 95 per cent confidence.

Before applying the t test, equality of variances has been tested with the F test. When the value of F showed that the variances differ from each other significantly, the statistic t that is adapted for comparison of samples having unequal variances has been used. It is assumed that the length and width of cheek teeth are normally distributed.

2.4. Nomenclature of the dental pattern.

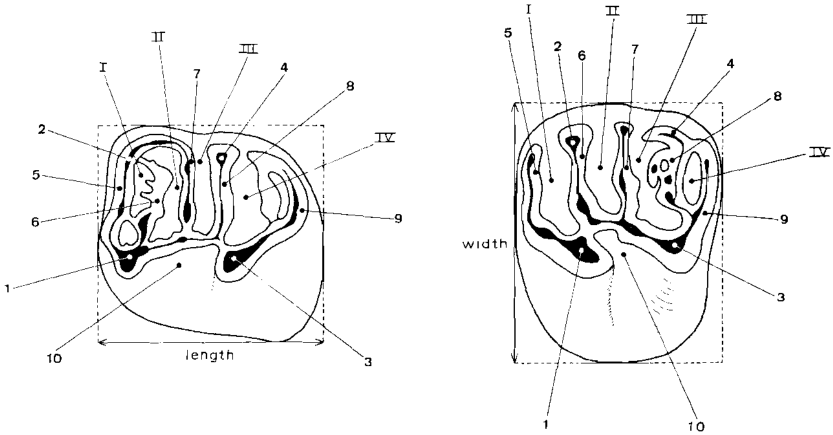
The nomenclature for portions of the dental patterns of the Pseudosciuridae and the Theridomyidae is shown in text-figs. 2 and 3. The same



Text-fig. 2 Nomenclature of the dental pattern of pseudosciurid cheek teeth.

lower cheek teeth	*upper cheek teeth*
1 protoconid	1 protocone
2 metaconid	2 paracone
3 hypoconid	3 hypocone
4 entoconid	4 metacone
5 anteroconid	5 protoconule
6 mesoconid	6 metaconule
7 hypoconulid	7 parastyle
8 mesostylid	8 mesostyle
9 ectostylid	9 anteroloph
10 anterolophid	10 protoloph
11 metalophid	11 metalophule I
12 entolophid	12 mesoloph
13 posterolophid	13 metaloph
14 ectolophid	14 posteroloph
15 antesinusid	15 endoloph
16 sinusid	16 sinus

nomenclature has been applied to the other rodents. Our nomenclature follows that of Wood and Wilson (1936).



M_{1-2} M^{1-2}

Text-fig. 3 Nomenclature of the dental pattern of theridomyid cheek teeth.

lower cheek teeth	*upper cheek teeth*
1 protoconid	1 protocone
2 metaconid	2 paracone
3 hypoconid	3 hypocone
4 entoconid	4 metacone
5 anterior branch metalophid	5 anteroloph
6 posterior branch metalophid	6 protoloph
7 mesolophid	7 mesoloph
8 entolophid	8 metaloph
9 posterolophid	9 posteroloph
10 sinusid	10 sinus
I synclinid I	I syncline I
II synclinid II	II syncline II
III synclinid III	III syncline III
IV synclinid IV	IV syncline IV

2.5. Terminology.

Some terms used frequently in this paper have several meanings in paleontological literature. Further explanation is given to four of these terms:

assemblage – collection of fossil remains from one locality, representing one particular taxon.

association – community of fossil species from one particular locality.

population – used in the statistical sense, as the measurements provided by a common characteristic of a set of objects.

sample – used in the statistical sense, as a subset of the population.

2.6. Storage.

The main part of the material that forms the basis of this study is stored in the Geologisch Instituut, Rijksuniversiteit Utrecht. Another part belongs to the collection of Mr. R. L. E. Ford (Yarmouth, Isle of Wight). The Theridomyidae from Lacey's Farm Quarry are kept in the Geological Museum of the University of Bristol.

2.7. Abbreviations.

The following abbreviations are used to indicate the collections in which specimens are housed:

B. M. (N. H.) – British Museum (Natural History), London.
B. S. P. G. – Bayerische Staatssammlung f. Paläontologie u. historische Geologie, München.
B. U. – Geological Museum, University of Bristol.
F. S. L. – Faculté des Sciences, Lyon.
F. C. – Collection R. L. E. Ford, Yarmouth, Isle of Wight.
G. I. U. – Geologisch Instituut, Rijksuniversiteit Utrecht.
I. S. B. – Institut royal des Sciences naturelles de Belgique, Bruxelles.
L. M. – Musée Géologique, Lausanne.
L. P. M. – Laboratoire de Paléontologie, Université de Montpellier.
M. N. H. N. – Muséum National d'Histoire Naturelle, Paris.
R. G. M. – Rijksmuseum van Geologie en Mineralogie, Leiden.
S. M. – Sedgwick Museum, Cambridge.
S. M. N. – Staatliches Museum f. Naturkunde, Stuttgart (Abteilung Ludwigsburg).

Specimens of the Ford-collection are additionally indicated by adding (FD) to the locality code, e.g. BC(FD).

The milk molars, permanent premolars and molars are indicated by D4, P4 and M1, M2 and M3, respectively.

The tables all apply to the material from the Isle of Wight, unless stated otherwise.

Chapter 3

LITHOSTRATIGRAPHY

3.1. Introduction.

The subdivision of the predominantly continental part of the Paleogene succession of the Isle of Wight as proposed by Forbes (1853) is generally followed by British stratigraphers. In the present paper the following units are regarded as formations:

Upper Hamstead Beds
Lower Hamstead Beds
Bembridge Marls
Bembridge Limestone
Osborne Beds
Upper Headon Beds
Middle Headon Beds
Lower Headon Beds

Barton Beds (marine)

For detailed descriptions of sections the reader is referred to Forbes (1853, 1856), Bristow, Reid and Strahan (1889), White (1921), Curry (1958) and Curry et al (1966).

Briefly, the lithological characteristics of the formations are as follows:

The *Lower Headon Beds* are composed of clay and marl with low carbonate content. They are of continental origin. The thickness is about 20 m.

The *Middle Headon Beds* have basal strata with marine fossils. These strata, often designated as the Brockenhurst Beds, are not present in the Headon Hill section. The Brockenhurst Beds are followed by a complex of partly bioturbate, partly laminated sands, clays and silts with lignitic layers. Pelecypod fossils are abundant and indicate a brackish-marine environment. The thickness of the Middle Headon Beds is about 10–15 m.

The lower part of the *Upper Headon Beds* consists of 5 m of calcareous marl with abundant freshwater molluscs. The top part is formed by 10 m of clay and silty clay, which are variegated in some places and contain freshwater molluscs. A 0.5 m thick lignitic layer occurs at 1–1.5 m from the base of the Upper Headon Beds at Headon Hill.

The *Osborne Beds* can hardly be distinguished from the Upper Headon Beds. They are usually recognized by being more varied in their lithological composition, including limestone, sand and clay. The thickness is approximately 25 m.

The *Bembridge Limestone* is a formation that has been extensively quarried as building-stone. It is essentially composed of compact cream-coloured limestone with some marl inclusions and contains freshwater molluscs. The thickness is about 5–8 m.

The *Bembridge Marls* consist of variegated marls and clays with freshwater molluscs. Locally they have an oyster bed at their base. The thickness varies from 25 m to 40 m.

The *Lower Hamstead Beds* are variegated clays with a "Black Band" (shale) at the base and a prominent "White Band" (layers of mollusc fragments) near the middle. The formation may reach a total thickness of about 75 m.

The *Upper Hamstead Beds* consist of about 10 m of very fossiliferous black or grey clays with a brackish-marine fauna.

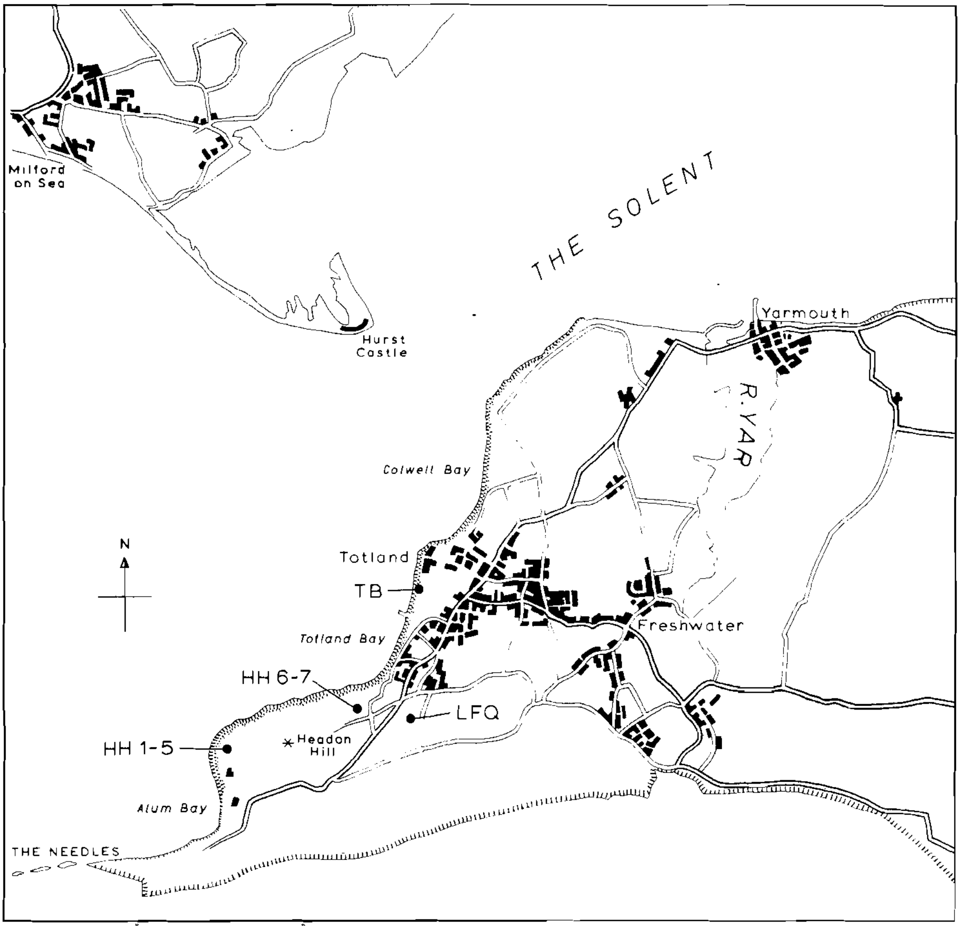
Fruits of *Chara* are locally present in the various formations.

3.2. **Lithostratigraphic position of the sampled localities.**

Rodent faunas have been collected from the cliff-sections at Headon Hill (Headon Hill 1–7), Totland Bay, Bouldnor Cliff and Whitecliff Bay (Whitecliff Bay 1, 2A and 2B) and from Lacey's Farm Quarry. The location of these exposures is indicated in text-figs. 4 and 5.

The larger part of the collecting has been done at Headon Hill. In this section the Lower Headon Beds up to and including the Bembridge Limestone are exposed. The levels at Headon Hill from which samples have been taken are numbered HH1 to HH7 from below upwards. Only HH1 to HH5 could be indicated in the stratigraphic column (text-fig. 6), which is composed of a number of exposures on the western slope of Headon Hill. The localities HH6 and HH7 are situated on the north-eastern slope of the hill and are somewhat difficult to correlate with HH1–5, because of overgrowth and because they occur in a formation that is not present in the western slope of Headon Hill.

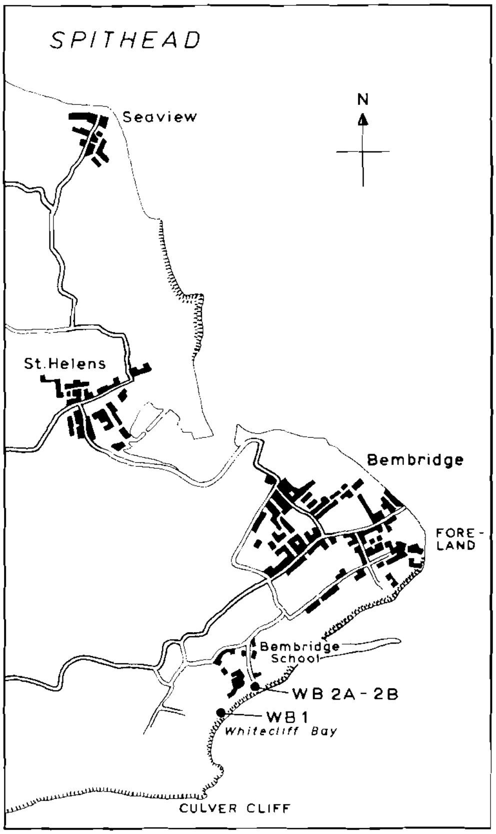
In the cliff-section at Whitecliff Bay the Lower Headon Beds up to and including the Bembridge Marls are exposed. Again, this section has a number of localities that can be placed in stratigraphic order. These localities are numbered WB1, WB2A and WB2B (text-fig. 6).



Text-fig. 4 The western part of the Isle of Wight, showing the location of the sampled localities.

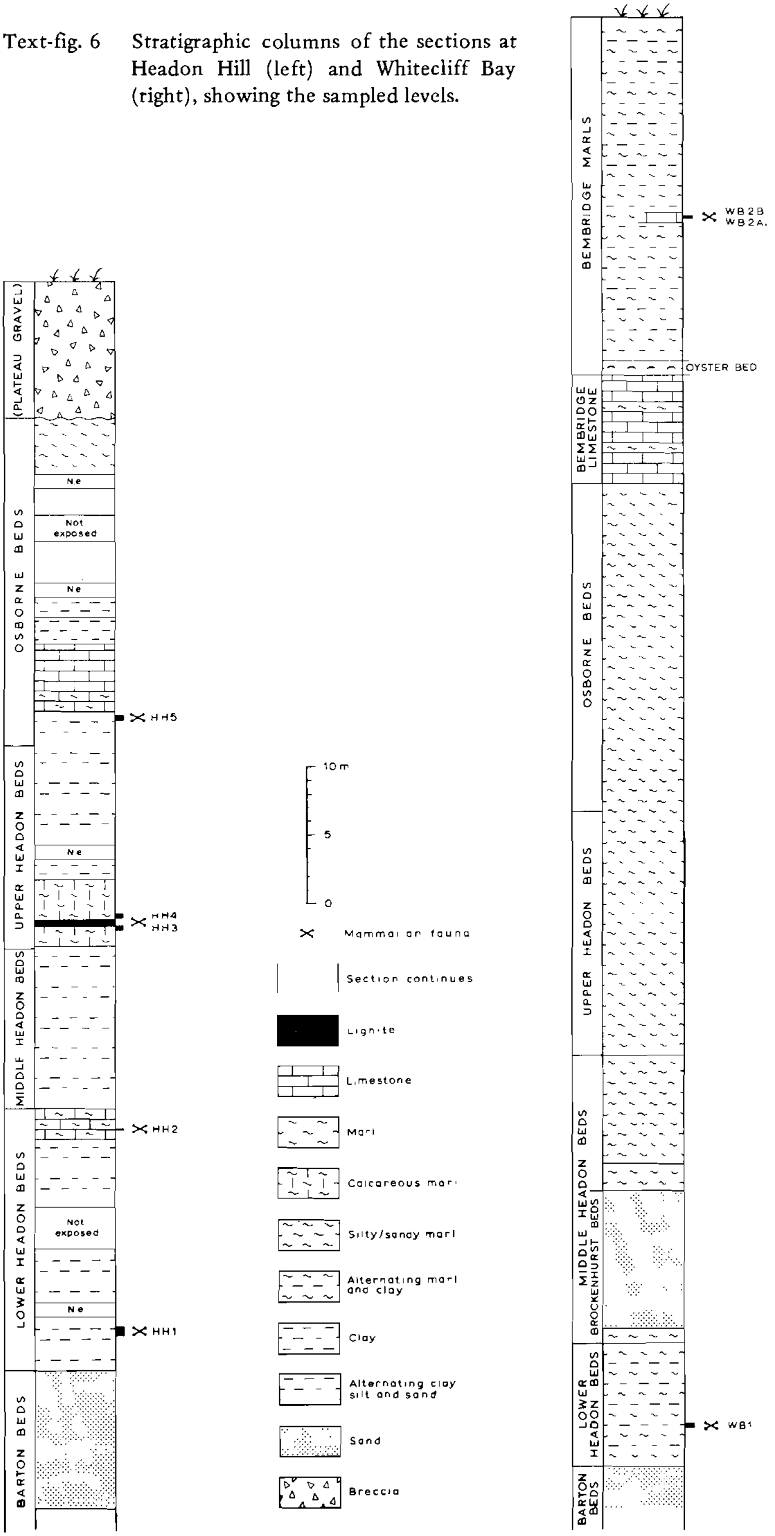
The Totland Bay (TB), Bouldnor Cliff (BC) and Lacey's Farm Quarry (LFQ) localities are not in a distinct lithological sequence with other localities, but can be placed in the general lithological sequence of the Isle of Wight.

The localities HH1–7, TB and BC are all situated in cliff-sections at the north-west coast of the island. To be brief, the exposures at this coast will be called together the Headon Hill-Bouldnor Cliff section.

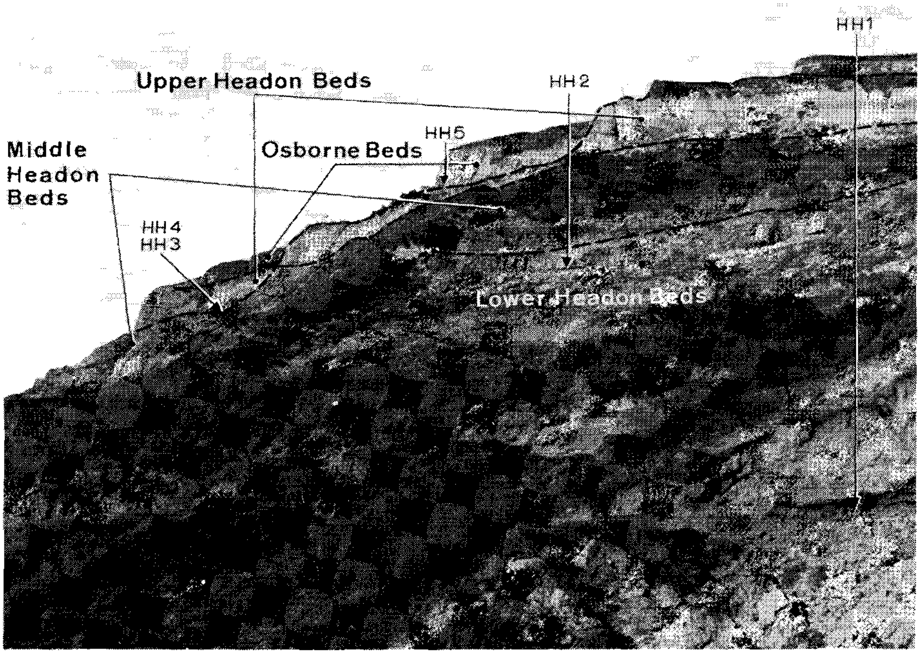


Text-fig. 5 The eastern part of the Isle of Wight, showing the location of the sampled localities.

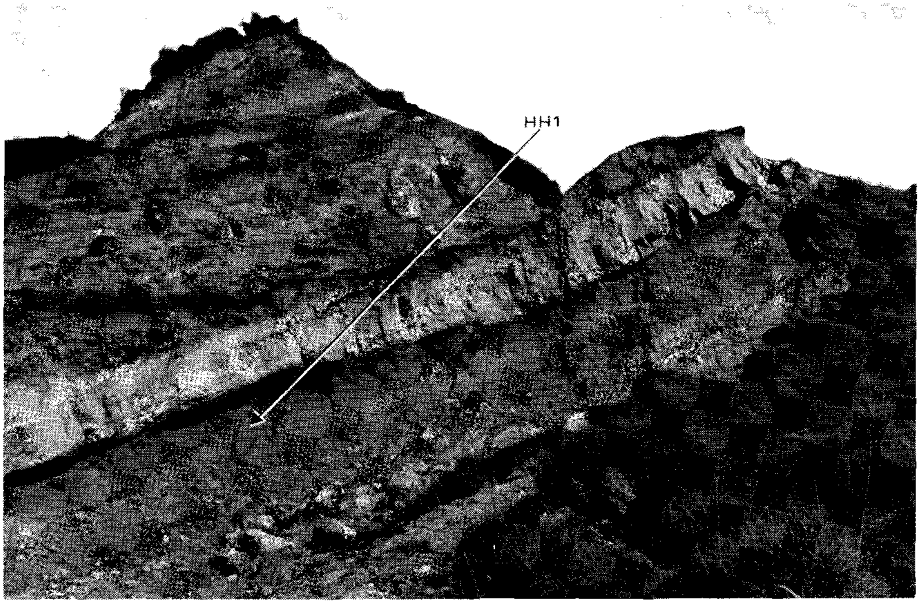
Text-fig. 6 Stratigraphic columns of the sections at Headon Hill (left) and Whitecliff Bay (right), showing the sampled levels.



3.2.1. Headon Hill-Bouldnor Cliff section.



Text-fig. 7 Section at the western slope of Headon Hill, showing the position of Headon Hill 1–5.



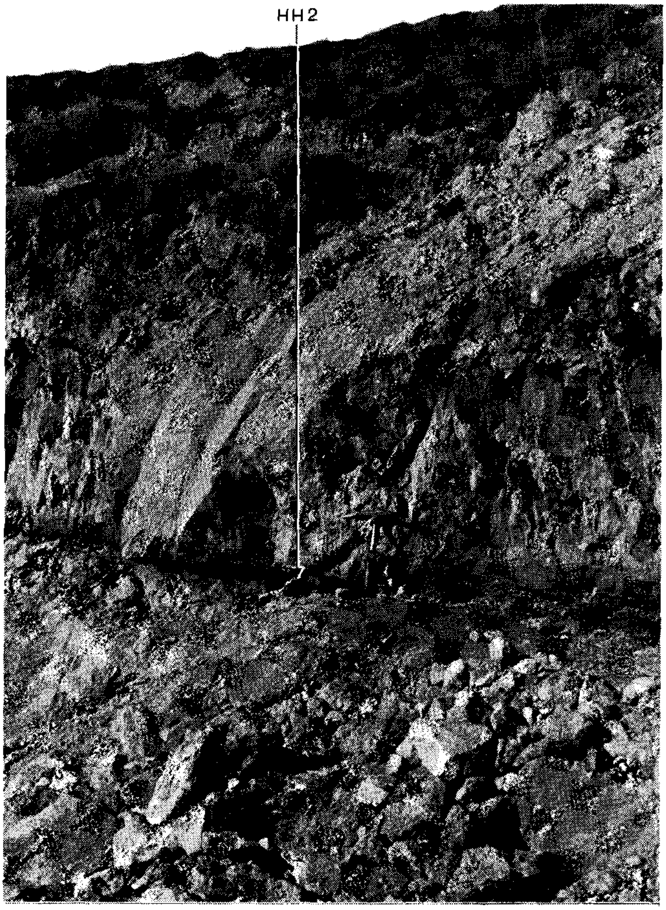
Text-fig. 8 Headon Hill 1.

HH1 (Lower Headon Beds) (text-figs. 6, 7 and 8).

Mammalian remains have been collected from a green silty clay with shell-fragments (thickness approximately 60 cm), which is exposed at about 2.5 m above the white sands marking the top of the Barton Beds.

HH2 (Lower Headon Beds) (text-figs. 6, 7 and 9).

Fossil material has been obtained from a green clay with *Limnaea* and *Planorbis* (thickness about 15 cm), which passes upwards into a lignitic clay (thickness approximately 5 cm). These strata are overlain by a pale brown marly limestone with *Limnaea* and *Planorbis,* approximately 1.4 m thick, which is prominent in the cliff and forms the top of the Lower Headon Beds.



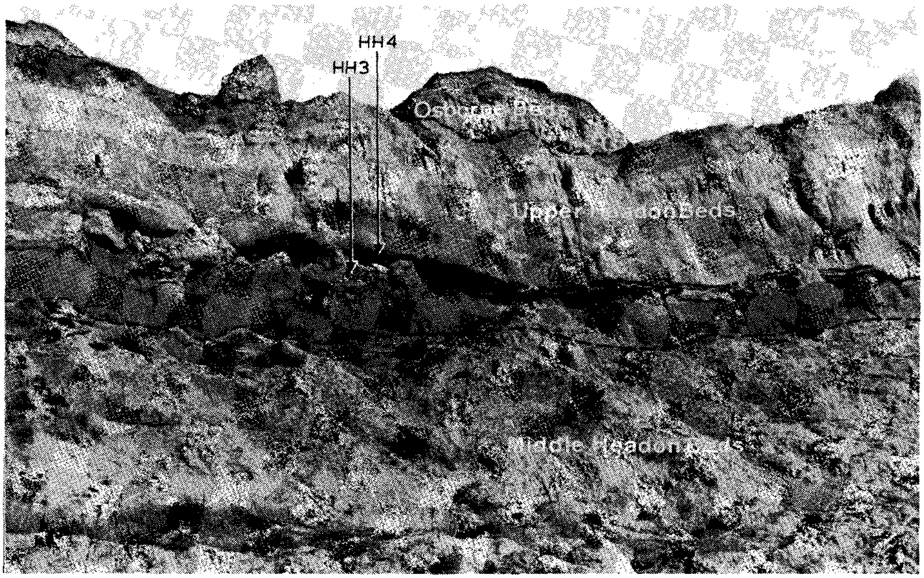
Text-fig. 9 Headon Hill 2.

HH3 and 4 (Upper Headon Beds) (text-figs. 6, 7 and 10).

HH3 refers to a chocolate-brown laminated silty marl with many shell-fragments (thickness variable, but maximally 30 cm), which is situated immediately below a lignite band of variable thickness (maximum 50 cm).

The HH4 material has been sampled from a grey-brown silty marl with shell-fragments (thickness variable, but maximally 15 cm), which is situated 20-30 cm above the same lignite band.

The silty marls are discontinuous. They are, together with the lignite band, intercalated in a chocolate-brown calcareous marl with *Limnaea, Planorbis* and *Hydrobia,* approximately 5 m thick, which forms a prominent cliff in the face of the hill.



Text-fig. 10 Headon Hill 3 and 4.

HH5 (Osborne Beds) (text-figs. 6, 7 and 11).

A few fossil teeth have been obtained from a grey-green silty clay, about 2.5 m thick, passing upwards into a soft white marly limestone (approximately 1.5 m thick). The sample has been taken at about 0.5 m below the marly limestone.

HH6 and 7 (Bembridge Limestone ?).

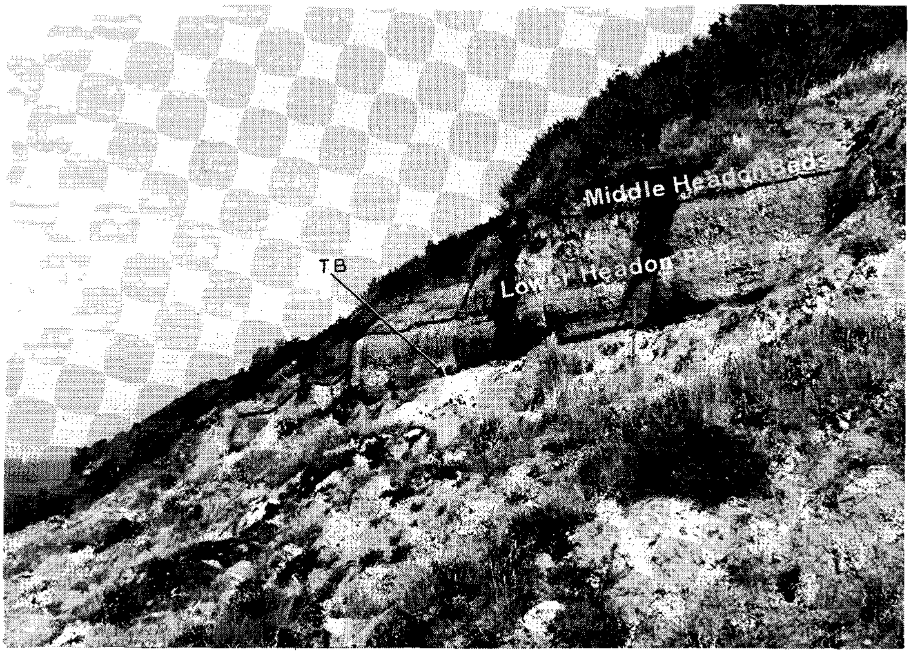
The localities are situated near the top of the cliff. On top of the main limestone succession of the Bembridge Limestone there is a unit, approximately 1.5 m thick and composed of marls, lignitic clays and lignites. This

Text-fig. 11 Headon Hill 5.

unit is overlain by pale yellow sand. Fossil material has been collected from lignitic clays with shell-fragments in the lower (HH6) and upper (HH7) parts of the unit, respectively. Edwards (1966) incorporated the marls, lignitic clays and lignites with the Bembridge Limestone.

Totland Bay (TB) (Lower Headon Beds) (text-fig. 12).

The locality is situated in the cliff at Totland Bay, 150–250 m north of the Pier. A mammalian fauna has been collected from a grey-green clay with shell-fragments (thickness approximately 8 cm), passing upwards into a lignitic clay (thickness approximately 2 cm). These layers are overlain by a pale brown marly limestone with *Limnaea* and *Planorbis*, about 1.5 m thick and prominent in the cliff. The sampled layer is considered to be a lateral equivalent of the layer of Headon Hill 2.



Text-fig. 12 Totland Bay.

Text-fig. 13 Bouldnor Cliff.

Bouldnor Cliff (BC) (Lower Hamstead Beds) (text-fig. 13).

The mammal collection of Mr. R. L. E. Ford has been made from thin bands of clay with fish and turtle remains, which can be seen in foreshore sections at low tide. The deposits are probably not *in situ,* but displaced by subrecent sliding movements.

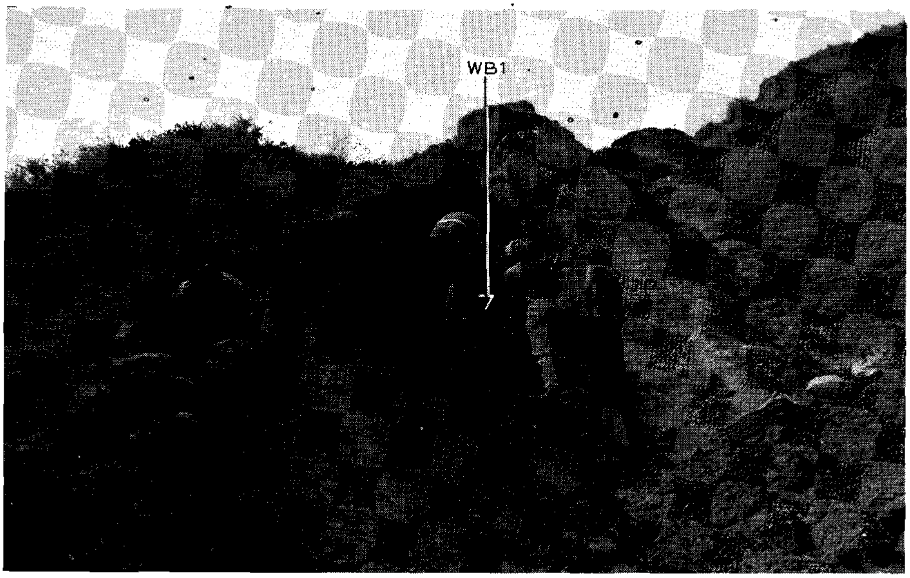
Headon Hill A, B and C (HH) (Upper Headon Beds).

Some cheek teeth are available in testing-samples from three localities on the western slope of Headon Hill, named Headon Hill A, B and C. These localities are situated in the Upper Headon Beds, below the main lignite band. Specimens from Headon Hill A, B and C are not involved in the statistical procedures.

3.2.2. **Whitecliff Bay** section.

WB1 (Lower Headon Beds) (text-figs. 6 and 14).

The locality is situated in the cliff at Whitecliff Bay, below the grounds of the Whitecliff Bay Hotel. Fossil material has been obtained from a lense of clay with abundant *Limnaea, Planorbis* and *Viviparus* (thickness approximately 25 cm), which is situated within green clay. This green clay (thickness about 2.0 m) passes upwards into a pure lignite. The lense is situated about 3 m above the russet sands here forming the top of the Barton Beds.

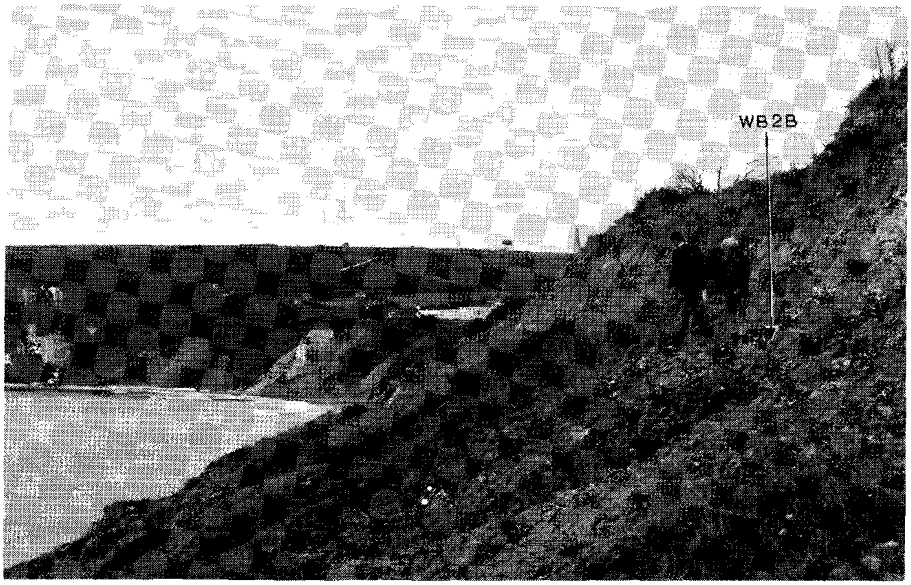


Text-fig. 14 Whitecliff Bay 1.

WB2A and B (Bembridge Marls) (text-figs. 6 and 15).

The localities WB2A and B are situated in the cliff at Whitecliff Bay, off Bembridge School. WB2A refers to a white marly limestone filling irregular depressions in the top of a solid limestone bed. Polished bone fragments are found concentrated in these depressions.

The WB2B material has been collected from a yellow marl (thickness approximately 20 cm), which is situated 5–10 m west of WB2A at about the same level. The beds are exposed at about 11.5 m above the main limestone succession of the Bembridge Limestone.



Text-fig. 15 Whitecliff Bay 2B.

3.2.3. Lacey's Farm Quarry, near Totland (LFQ) (Osborne Beds).

This locality is University of Bristol site no. 6911. The succession in this quarry consists of rubbly limestones with thin irregular clay or marl layers at intervals. These layers contain abundant calcareous concretions. Lacey's Farm Quarry has yielded mammalian remains at two levels (Bosma and Insole, 1972). The rodent fauna of the upper level is included in this paper.

Chapter 4

TAXONOMY

4.1. Family PSEUDOSCIURIDAE Zittel, 1893

Introduction.

Usually two families are distinguished within the superfamily Theridomyoidea (= suborder Theridomorpha of some authors), viz. the Pseudosciuridae and the Theridomyidae Alston, 1876. This distinction is maintained, because considerable differences in dental pattern are found between the majority of the species of the two families. Hartenberger (1971) discovered species that are contiguous to the Pseudosciuridae as well as to the Theridomyidae. These species may be classified with one family or the other in an arbitrary way.

The present author does not recognize subfamilies within the Pseudosciuridae. This is in full agreement with the conclusions of Schmidt-Kittler (1971).

4.1.1. Genus **Sciuroides** Major, 1873

Original reference: Major (1873), p. 79.
Subsequent reference: Schmidt-Kittler (1971), p. 29.
Type-species: Sciurus siderolithicus Pictet and Humbert, 1869.

4.1.1.1. **Sciuroides ehrensteinensis** Schmidt-Kittler, 1971 (Plate V, figs. 1–6)

Original reference: Schmidt-Kittler (1971), p. 37–38; fig. 15; plate I, fig. 7.
Synonymy: Sciuroides A n. sp.: Schmidt-Kittler (1971), p. 35, 37; fig. 14.

Emended diagnosis:

A *Sciuroides* species with large cheek teeth. Main cusps prominent. Anteroconid usually connected with the metalophid. Metalophule I usually connected with the endoloph.

Holotype: An isolated M^{1-2} (B.S.P.G. 1968 VII–742).

Type-locality: Ehrenstein (Fed.Rep. Germany).

Stratigraphic range on the Isle of Wight: Lower Headon Beds, Upper Headon Beds.

Material:
Headon Hill 1: 1 M_{1-2}, 1 M^{1-2}.
Headon Hill 2: 1 P_4, 1 M_{1-2}, 1 D^4, 6 M^{1-2}.
Totland Bay: 1 M_{1-2}, 1 M^{1-2}.
Headon Hill 3: 1 M_3.
Headon Hill A, B or C: 1 M_{1-2}.

Measurements: see table I.

	Locality	Length			Width		
		N	range	$\bar{X}$	N	range	$\bar{X}$
M_{1-2}	Headon Hill 2	1	–	31.5	1	–	27.1
M_3	Headon Hill 3	1	–	28.9	1	–	21.7
D^4	Headon Hill 2	1	–	30.6	1	–	28.6
M^{1-2}	Headon Hill 2	3	30.7 – 31.9	31.47	3	31.0 – 32.0	31.50
	Headon Hill 1	1	–	29.2	–	–	–

Table I. Measurements of the cheek teeth of *Sciuroides ehrensteinensis* Schmidt-Kittler, 1971 (N = number of observations, $\bar{X}$ = mean value).

Description:

P_4: The only P_4 available is very worn. The tooth shows the four main cusps and an entolophid and posterolophid. The junction of the ectolophid and the entolophid is clearly separated from the hypoconid. The ectolophid bears a well-developed mesoconid.

M_{1-2}, M_3: The metaconid and entoconid are conical and higher than the protoconid and hypoconid. The metalophid, entolophid, posterolophid and ectolophid are conspicuous. The sinusid is trapezium-shaped, since the posterior half of the ectolophid runs parallel to the buccal side of the tooth. The junction of the ectolophid and the entolophid is separated from the hypoconid. The ectolophid bears a mesoconid of variable size. The posterolophid may bear a hypoconulid (Plate V, fig. 1). The anteroconid is usually connected with the metalophid, forming an antesinusid. The enamel is slightly rugose.

D^4, M^{1-2}: The four main cusps are prominent. The protoconule is well delimited and elongated antero-posteriorly, reaching to the anterior side of the protoloph. The metaconule is a large circular cusp, which is connected with the metacone, but separated from the hypocone. The sinus is more or less symmetrical. The metalophule I is complete in some specimens, but it is interrupted in others. The anteroloph and posteroloph show swellings at the antero-buccal side of the protocone and the postero-buccal side of the hypocone respectively. Usually there is a small mesostyle, which is connected with the paracone. The mesostyle and metacone are separated by a deep incision. In some specimens the mesostyle is developed as a short mesoloph (Plate V, figs. 5 and 6). The posterior wall of the tooth usually presents a furrow at the postero-buccal side of the hypocone. The enamel is slightly rugose. The single D^4 differs from the M^{1-2} by its conspicuous parastyle, which is separated from the paracone by an incision.

Discussion:

Differences between *Sciuroides* A, *S. ehrensteinensis* and the *Sciuroides* M^{1-2} from the Isle of Wight are thought to fall within the range of variation of one species. Therefore, the assemblages from the Isle of Wight are given the specific determination *S. ehrensteinensis,* while *Sciuroides* A is considered to be synonymous with *S. ehrensteinensis.*

Remark:

Suevosciurus (Treposciurus) romani Hartenberger, 1973 shows close similarity in dental pattern to *Sciuroides siderolithicus* and *S. ehrensteinensis* and had better be included in *Sciuroides.*

4.1.2. Genus **Suevosciurus** Dehm, 1937

Original reference: Dehm (1937), p.273, p.275-276.
Subsequent reference: Schmidt-Kittler (1971), p.39.
Type-species: Sciuroides fraasi Major, 1873.

4.1.2.1. **Suevosciurus palustris** (Misonne, 1957) (Plate V, figs. 7–9)

Original reference: Adelomys palustris Misonne, 1957; p.2, p.4; plate II, fig. 3.

Diagnosis:

A *Suevosciurus* species with cheek teeth that are intermediate in size between those of *Suevosciurus minimus* and *Suevosciurus fraasi:* 1.45 mm $<$ mean length $M_{1-2} < 1.75$ mm.

Holotype: An isolated M^{1-2} (I.S.B. Ht. M. 1144).

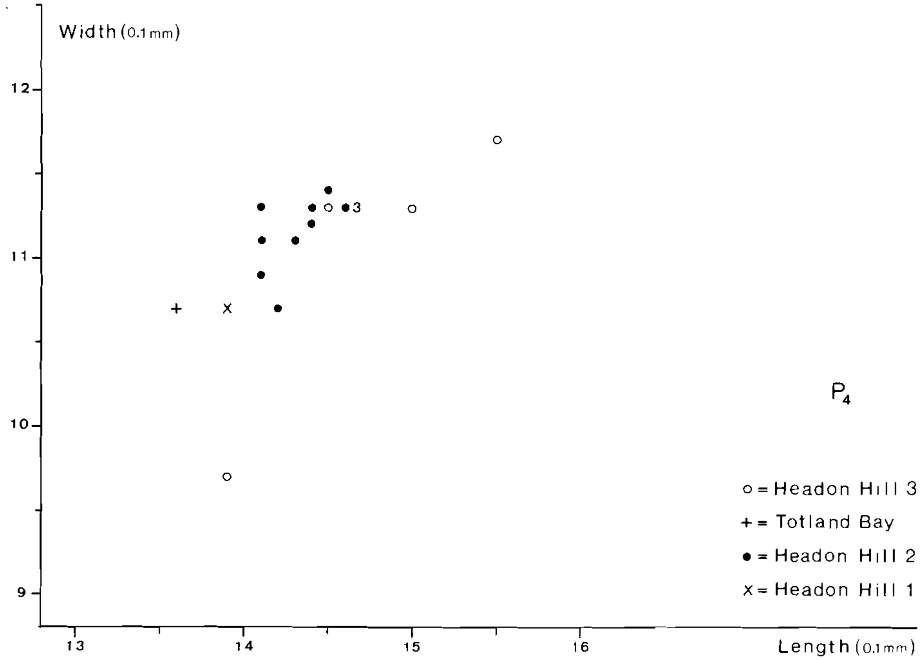
Type-locality: Hoogbutsel (Belgium).

Stratigraphic range on the Isle of Wight: Lower Headon Beds, Upper Headon Beds.

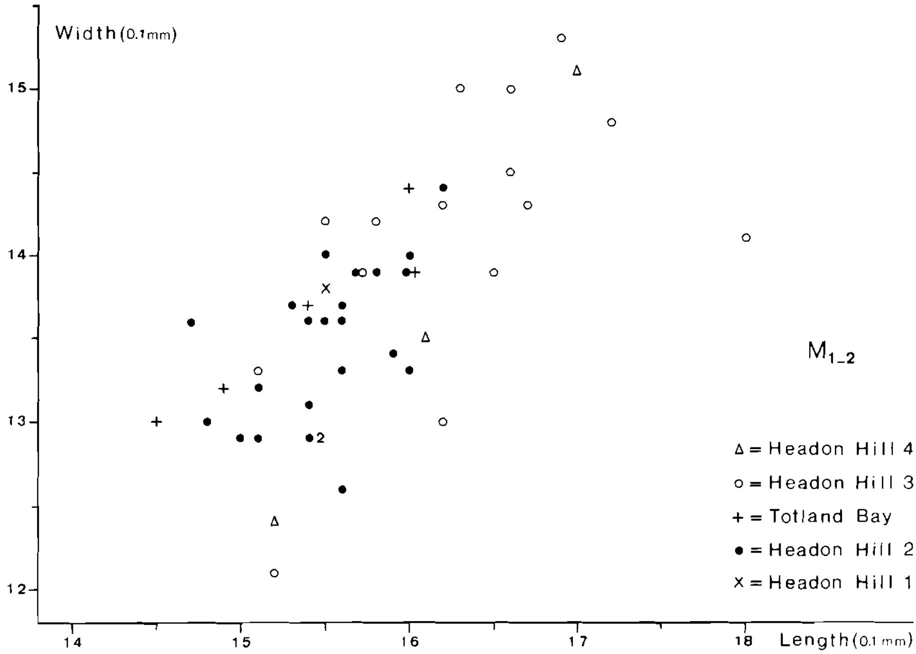
Material:
Headon Hill 1: 1 P_4, 1 M_{1-2}, 1 P^4.
Headon Hill 2: 11 P_4, 25 M_{1-2}, 7 M_3, 15 P^4, 36 M^{1-2}, 15 M^3.
Totland Bay: 1 P_4, 5 M_{1-2}, 3 M_3, 3 P^4, 3 M^{1-2}, 2 M^3.

	Locality	Length					Width		
		N	range	$\bar{X}$	s	confidence interval	N	range	$\bar{X}$
P_4	Headon Hill 3	4	13.9–15.5	14.73	0.68	$13.64 < \mu < 15.82$	5	9.7–11.7	10.98
	Totland Bay	1	–	13.6	–	–	1	–	10.7
	Headon Hill 2	11	14.1–14.6	14.35	0.21	$14.21 < \mu < 14.49$	11	10.7–11.4	11.17
	Headon Hill 1	1	–	13.9	–	–	1	–	10.7
M_{1-2}	Headon Hill 4	3	15.2–17.0	16.10	0.90	$13.87 < \mu < 18.33$	3	12.4–15.1	13.67
	Headon Hill 3	16	15.1–18.5	16.44	0.93	$15.95 < \mu < 16.93$	16	12.1–15.3	14.09
	Totland Bay	5	14.5–16.0	15.36	0.67	$14.53 < \mu < 16.19$	5	13.0–14.4	13.64
	Headon Hill 2	25	14.7–16.3	15.55	0.41	$15.38 < \mu < 15.72$	23	12.6–14.4	13.45
	Headon Hill 1	1	–	15.5	–	–	1	–	13.8
M_3	Headon Hill 3	13	15.8–18.3	17.28	0.70	$16.85 < \mu < 17.71$	10	12.9–14.2	13.70
	Totland Bay	3	16.4–16.6	16.53	0.12	$16.24 < \mu < 16.82$	2	13.1–13.2	13.15
	Headon Hill 2	7	15.7–16.8	16.20	0.37	$15.86 < \mu < 16.54$	7	12.9–13.8	13.27
P^4	Headon Hill 4	1	–	17.0	–	–	1	–	14.1
	Headon Hill 3	8	15.8–16.4	16.03	0.21	$15.86 < \mu < 16.20$	8	13.3–14.2	13.71
	Totland Bay	2	15.9–16.6	16.25	0.49	$11.80 < \mu < 20.70$	3	12.3–14.5	13.40
	Headon Hill 2	15	14.5–16.1	15.20	0.48	$14.94 < \mu < 15.46$	15	12.8–14.4	13.53
M^{1-2}	Headon Hill 4	4	14.8–15.6	15.20	0.41	$14.55 < \mu < 15.85$	3	14.5–14.8	14.60
	Headon Hill 3	21	14.7–16.7	15.83	0.59	$15.56 < \mu < 16.10$	18	14.3–16.8	15.52
	Totland Bay	3	14.4–15.0	14.73	0.31	$13.97 < \mu < 15.49$	3	14.5–14.8	14.70
	Headon Hill 2	36	13.9–16.3	15.11	0.53	$14.93 < \mu < 15.29$	32	13.7–16.0	14.82
M^3	Headon Hill 4	1	–	13.6	–	–	1	–	14.2
	Headon Hill 3	11	12.6–16.7	14.57	1.15	$13.80 < \mu < 15.34$	9	14.0–17.2	15.23
	Totland Bay	2	12.9–14.4	13.65	1.06	$4.12 < \mu < 23.18$	2	13.6–14.0	13.80
	Headon Hill 2	15	12.5–14.9	13.87	0.77	$13.44 < \mu < 14.30$	15	12.9–14.7	13.88

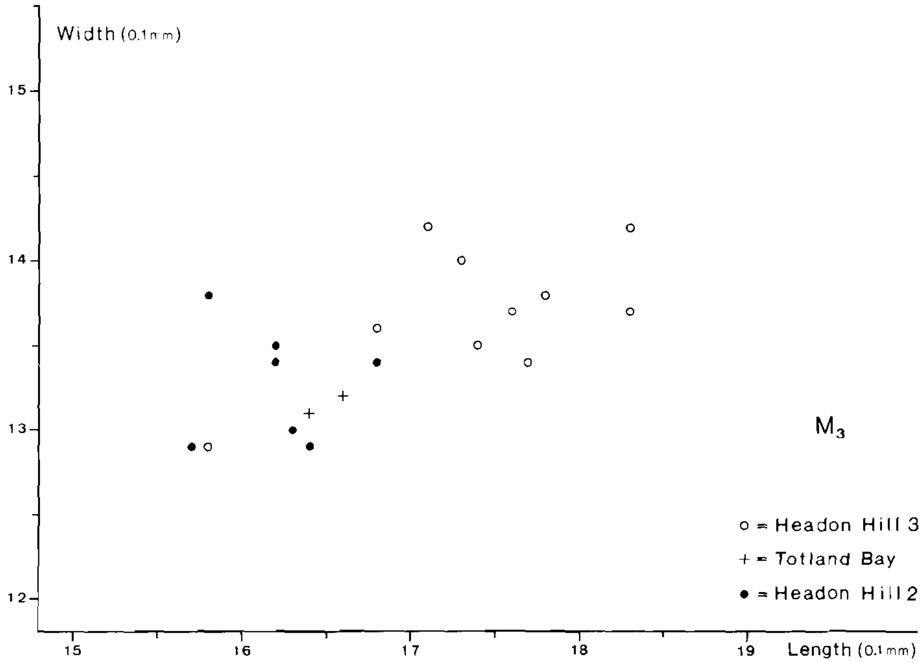
Table II. Measurements of the cheek teeth of *Suevosciurus palustris* (Misonne, 1957) and confidence interval estimates of the population means (of the length only). (N = number of observations, $\bar{X}$ = mean value, s = standard deviation of the sample).



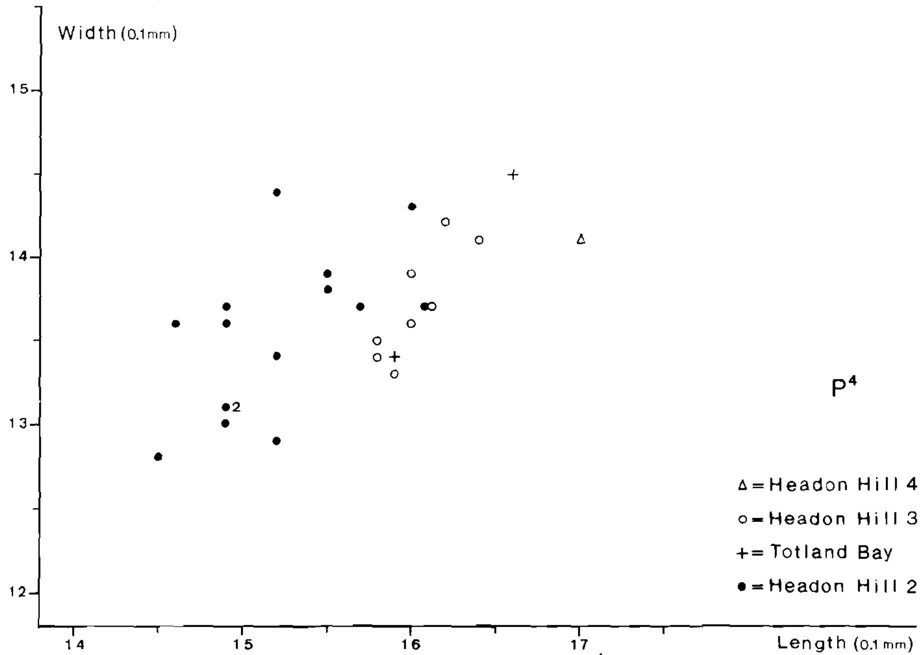
Text-fig. 16 Scatter diagram showing length and width of the P_4 of *Suevosciurus palustris* (Misonne, 1957).



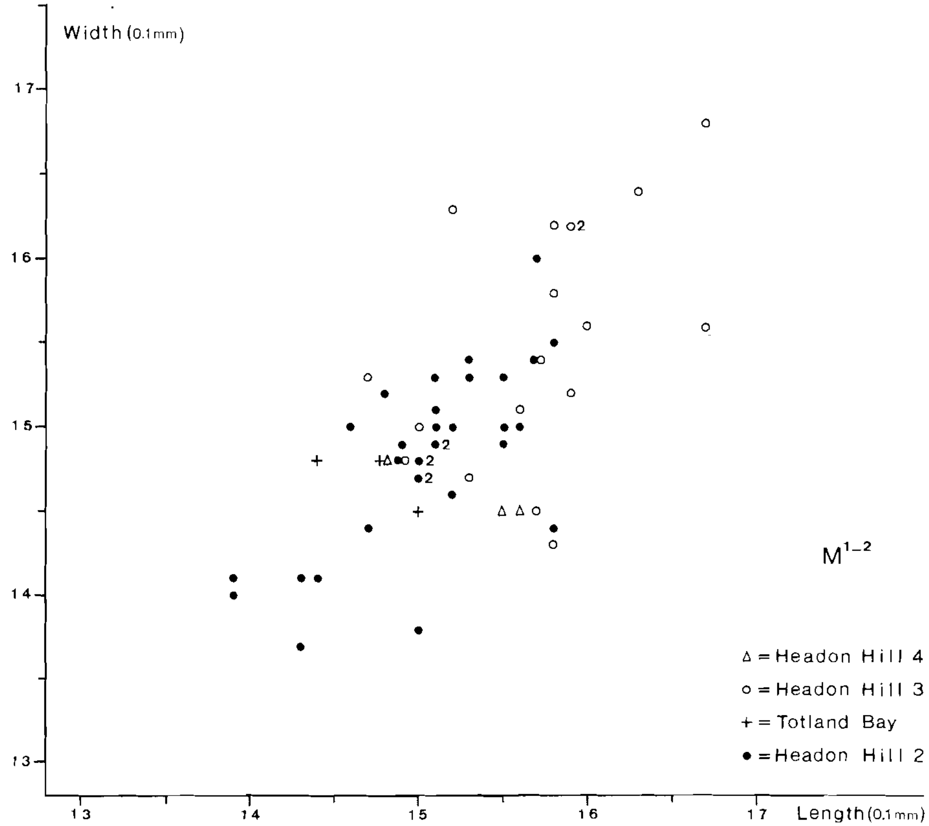
Text-fig. 17 Scatter diagram showing length and width of the M_{1-2} of *Suevosciurus palustris* (Misonne, 1957).



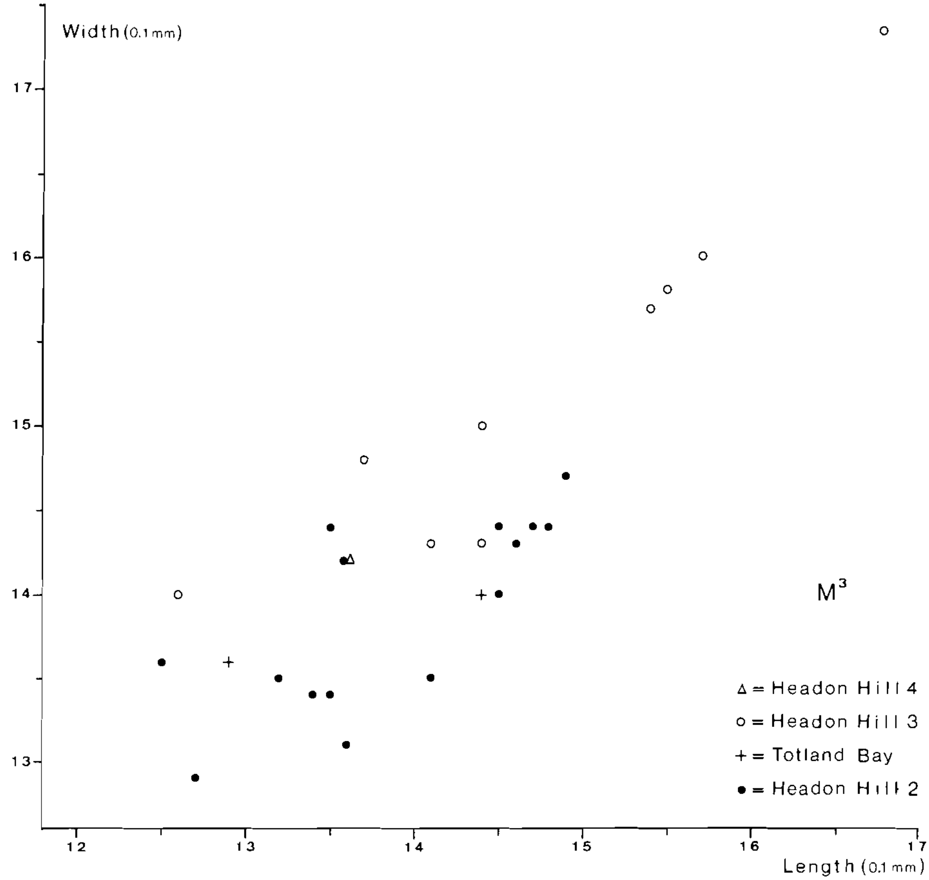
Text-fig. 18 Scatter diagram showing length and width of the M_3 of *Suevosciurus palustris* (Misonne, 1957).



Text-fig. 19 Scatter diagram showing length and width of the P^4 of *Suevosciurus palustris* (Misonne, 1957).



Text-fig. 20 Scatter diagram showing length and width of the M^{1-2} of *Suevosciurus palustris* (Misonne, 1957).



Text-fig. 21 Scatter diagram showing length and width of the M^3 of *Suevosciurus palustris* (Misonne, 1957).

Headon Hill 3: 5 P_4, 17 M_{1-2}, 13 M_3, 8 P^4, 21 M^{1-2}, 11 M^3.
Headon Hill 4: 3 M_{1-2}, 1 P^4, 4 M^{1-2}, 1 M^3.
Headon Hill B: 3 P^4, 4 M^{1-2}, 2 M^3.
Headon Hill C: 1 M_{1-2}, 1 M_3, 1 P^4, 2 M^{1-2}, 1 M^3.

Measurements: see table II and text-figs. 16–21.

Description of the material and discussion of the morphology of some specimens:

The dental pattern of *S. palustris* from the Isle of Wight and its variability are very similar to those of *S. fraasi* (Major, 1873), *S. ehingensis* Dehm, 1937 and *S. minimus* (Major, 1873). These species, which differ mainly in size, have been extensively described and figured by Schmidt-Kittler (1971). Therefore, particular attention will be given to those features of the English material not described by Schmidt-Kittler.

P_4: The structure of the anterolophid/anteroconid shows much variation. In some specimens it consists of a slight swelling at the anterior wall of the tooth only, while in other specimens it consists of a crest, the length of which is at least half of the distance between protoconid and metaconid. This crest is either connected to the protoconid or metaconid, or it is separated from these cusps. Two specimens show a distinct anteroconid, which is connected to the metalophid.

M_{1-2}: In all specimens the anterolophid bears a low anteroconid, which is separated from the protoconid by a deep incision. Occasionally there is an indistinct connection between the anteroconid and the metalophid. This connection is also present in the M_1 and M_2 of the holotype of *S. minimus* (see Schmidt-Kittler (1971), p. 48; fig. 21a). The absence of a connection between the anteroconid and metalophid should therefore not be used as a diagnostic character of *Suevosciurus,* as done by Schmidt-Kittler (1971, table 4).

The metalophid may show a swelling in the middle, while a mesostylid may be present between the metaconid and entoconid. In one specimen the ectolophid differs from the typical *Suevosciurus* configuration in that it reaches the entolophid separate from the hypoconid (Plate V, fig. 7).

The dental pattern of another specimen (Plate V, fig. 8) is considerably different from the usual pattern of *Suevosciurus* M_{1-2}. In addition to the four main cusps, two cusps are present at the antero-buccal and postero-lingual sides of the hypoconid respectively. Moreover, the metalophid, entolophid and ectolophid are missing, while the posterolophid is weak. In spite of this aberrant pattern, the tooth is considered to belong to *S. palustris,* because of its almost identical size, the same position of its main cusps, the similar structure of its anterolophid and the rugosity of its enamel, which is common in *Suevosciurus* cheek teeth.

M_3: The anterolophid often bears an anteroconid. In some specimens the anterolophid and the protoconid are connected. In M_3 the enamel is usually more corrugated than in M_{1-2}.

P^4: The parastyle is usually more or less bicuspidate.

M^{1-2}: Unlike in most M^{1-2}, the protoloph is interrupted in the middle in one specimen. In another specimen the metaloph is absent, while the metacone is connected to the middle of the posteroloph by a conspicuous ridge. These features are also present in a M^{1-2} of *S. minimus* from Ehrenstein I (A) (Fed. Rep. Germany), figured by Schmidt-Kittler (1971, fig. 21b). In two M^{1-2} the posteroloph is interrupted at its lingual side. The mesostyle is of variable prominence, but usually it is relatively high. Occasional specimens show a short ridge coming from the endoloph and directed toward the metacone. This usually low ridge at most extends to half-way the central valley (Plate V, fig. 9).

M^3: Often a well-developed mesostyle is present.

In spite of the availability of abundant *Suevosciurus* material from Southern Germany and the Isle of Wight, no distinction could be made between milk molars and permanent premolars. D^4 in the Pseudosciuridae are usually characterized by their strong parastyle *(Sciuroides, Treposciurus, Paradelomys).* In contrast, *Suevosciurus* teeth with such a cusp are considered to be P^4, as their pattern, apart from the parastyle, very closely resembles that of the molars. Moreover, their height and the size and orientation of their roots are similar to those in M^{1-2}. It cannot be excluded that the premolars are milk molars persisting throughout life.

Comparison of the lengths of the cheek teeth:

The phylogenetical development of the *Suevosciurus* species is thought to be characterized by an increase in the size of the cheek teeth (Schmidt-Kittler, 1971). Whether this increase in size also occurs in *S. palustris* from the Isle of Wight has been studied by the determination of confidence intervals for estimating the population means of the length, and by testing the differences in mean length with the statistic t. Confidence intervals are given in table II, values of t in table III.

From these tables it can be concluded that there is a significant increase in length of M_{1-2}, M_3, P^4 and M^{1-2} between Headon Hill 2 and 3; of P^4 between Headon Hill 2 and 4; of M_{1-2} and M^{1-2} between Totland Bay and Headon Hill 3; of P^4 between Headon Hill 3 and 4. The P^4 from Totland Bay are significantly longer than the P^4 from Headon Hill 2, but the opposite is found in the P_4.

	P_4	M_{1-2}	M_3	P^4	M^{1-2}	M^3
HH3–HH4	–	0.585(17)	–	*4.455(7)*	2.019(23)	0.808(10)
TB–HH4	–	1.348(6)	–	1.237(1)	1.661(5)	0.039(1)
TB–HH3	1.476(3)	*2.399*(19)	1.794(14)	1.071(8)	*3.112*(22)	1.049(11)
HH2–HH4	–	1.046(3.15)	–	*3.657*(14)	0.330(38)	0.339(14)
HH2–HH3	1.092(4.27)	*3.620*(20.18)	*3.760*(18)	*5.811*(23.11)	*4.756*(55)	1.862(24)
HH2–TB	*3.474*(10)	0.853(28)	1.470(8)	*2.919*(15)	1.224(37)	0.368(15)
HH1–HH4	–	0.577(2)	–	–	–	–
HH1–HH3	1.084(3)	0.983(15)	–	–	–	–
HH1–TB	–	0.192(4)	–	–	–	–
HH1–HH2	2.084(10)	0.120(24)	–	–	–	–

Table III. t values for comparison of the mean length of the cheek teeth of *Suevosciurus palustris* (Misonne, 1957) (Numbers of degrees of freedom in parentheses; significant values of t in italics).

Discussion of the phylogenetical position of Suevosciurus palustris:

The cheek teeth of *S. palustris* do not differ morphologically from those of other *Suevosciurus* species and are intermediate in size between the cheek teeth of *S. minimus* and *S. fraasi.* From Schmidt-Kittler's (1971) fig. 20 it can be deduced that the mean length of the M_1 and M_2 in the holotype of *S. minimus* amounts to 13.5; the mean length of M_1 and M_2 in the three dentitions of *S. fraasi* from Örlinger Tal (Fed. Rep. Germany), among which is the holotype (S.M.N. St. 14), amounts to 19.2. Schmidt-Kittler's fig. 20 as well as our *S. palustris* assemblages from the Isle of Wight show that the range of the length of M_{1-2} in *Suevosciurus* species is approximately 20 per cent of the mean value at the utmost. Hence the length of M_{1-2} in the type-assemblages of *S. minimus* and *S. fraasi* may be estimated to range from 12.2 to 14.9 and from 17.3 to 21.1, respectively. In the absence of diagnostic characters other than size, we propose to distinguish between *S. minimus, S. palustris* and *S. fraasi* on the basis of the mean length of M_{1-2} and to fix the limits between the three species arbitrarily at 14.5 (= 1.45 mm) and 17.5 (= 1.75 mm).

With these limits the allocation of the assemblage from Headon Hill 4 to *S. palustris* remains doubtful. Because of the low number of data the lower and upper confidence limits of the mean length of M_{1-2} fall within the ranges of *S. minimus* and *S. fraasi* respectively.

The fourth *Suevosciurus* species, *S. ehingensis,* is considerably larger than *S. fraasi.* Material of *S. ehingensis* from the type-locality, Ehingen 1, is limited to one P^4 and one M^{1-2}. If it is assumed, that the lengths of M^{1-2} and M_{1-2} of *S. ehingensis* are in proportion in the assemblages from Ehingen 1, Ehrenstein 1 (B) and Herrlingen 1 (Fed. Rep. Germany), the mean length of M_{1-2} from Ehingen 1 would be approximately 29 (from Schmidt-Kittler's fig. 20). If the range of the length is estimated at about 20 per cent of the mean value, the minimal length of M_{1-2} would approximate to 26. As the upper limit of the range of the length of M_{1-2} in the type-assemblage of *S. fraasi* may be estimated at 21.1, there seems to be room left for a fifth *Suevosciurus* species, which is intermediate in size between *S. fraasi* and *S. ehingensis.*

Schmidt-Kittler (1971) recognized two lineages of the genus *Suevosciurus* in a number of localities in Southern Germany that he considered to belong to the mammalian "zones" of Montmartre, Frohnstetten, Ronzon and La Sauvetat. These lineages are thought to show parallel evolution, with the cheek teeth undergoing a gradual increase in size. When Schmidt-Kittler could ascertain the presence of species of both lineages in one locality from the clusters in his scatter diagrams (fig. 20), he referred the smaller species to *S. fraasi* and the larger one to *S. ehingensis.*

A different classification, which is based on the mean length of M_{1-2}, is given in table IV. In Mormont-Entreroches (Switzerland), Ehrenstein 1 (A) and Weissenburg 6 *Suevosciurus* is only represented by *S. minimus,* in Bernloch 1 (B), Ehingen 1 and Echelsbacher Brücke only by *S. ehingensis.* In the remaining localities either *S. palustris* occurs together with *S. fraasi* or a *Suevosciurus* species that is intermediate in size between *S. fraasi* and *S. ehingensis,* or *S. fraasi* occurs together with the latter species or *S. ehingensis.*

According to this classification, *S. fraasi* from Weissenburg 8 is a member of the lineage consisting of the larger forms, whereas *S. fraasi* from Möhren 6, Örlinger Tal, Bernloch 1 (A), Ronheim 1, Herrlingen 1 and Schelklingen 1 are members of the lineage consisting of the smaller forms. Therefore, the insertion of an assemblage in a particular lineage is only possible if two species are present in one locality. If only one species is present, its phylogenetical position might be ascertained from the associated fauna.

The cheek teeth of *S. palustris* from the Headon Beds are smaller than those of *S. palustris* from Weissenburg 8 and 2 and Ehrenstein 1 (B); it is self-evident that they are also smaller than the cheek teeth of *S. fraasi.* If it is

	S. minimus	*S. palustris*	*S. fraasi*	*S. ehingensis*	
				S. ?n.sp.	*S. ehingensis*
Mean length of M_{1-2}	< 14.5	14.5–17.5	17.5–21.1	21.1–26.0	> 26.0
Locality					
Echelsbacher Brücke					x
Ehingen 1					x*)
Bernloch 1(B)					x*)
Schelklingen 1			x*)		x
Herrlingen 1			x		x
Ronheim 1			x		x
Ehrenstein 1(B)		x		x	
Bernloch 1(A)			x	x*)	
Weissenburg 2		x		x	
Örlinger Tal			x	x	
Möhren 6			x	x	
Weissenburg 8		x	x		
Weissenburg 6	x				
Ehrenstein 1(A)	x				
Mormont-Entreroches	x				

Table IV. Classification of *Suevosciurus* assemblages from Southern Germany and Switzerland according to the mean length of the M_{1-2}. (Measurements after Schmidt-Kittler (1971), fig. 20) (*) Classification based on M^{1-2}).

assumed that *S. palustris* shows a general increase in size, the localities Headon Hill 1–4 and Totland Bay would be older than Weissenburg 8 (see table IV and Schmidt-Kittler's table 8).

Remarks:

The limited number of specimens available from Hoogbutsel: 2 M_{1-2} and 4 M^{1-2} (Institut royal des Sciences naturelles de Belgique), 1 M^{1-2} (G.I.U. HB 801) and 1 M^3 (R.G.M. St. 149.063), and their rather poor state of preservation do not permit detailed comparison with the material from the Headon Beds. G.I.U. HB 801 shows a structure unknown to the material from the Isle of Wight. In this tooth the endoloph is interrupted at the buccal side of the sinus, while the mesostyle is hardly developed.

A very worn M^3 of *Suevosciurus* has been collected from Headon Hill 6. This specimen could not be measured accurately, but it belongs either to *S. fraasi* or to *S. palustris*. The species is indicated in the range and correlation charts (text-figs. 37 and 38) as *Suevosciurus* sp.

There is much similarity in dental pattern between our material and the teeth from Escamps (France) Hartenberger (1973) referred to as *Suevosciurus (Microsuevosciurus)* sp. indet. Although Hartenberger detached his material from *S. fraasi, S. palustris* and *S. minimus,* it is, in our opinion, closely related to these species. Judging by the size of the figured P^4 (Hartenberger (1973), plate I, fig. 14) the species from Escamps has to be classified either as *S. palustris* or as *S. fraasi.*

4.1.3. Genus Treposciurus Schmidt-Kittler, 1970

Original references: Schmidt-Kittler (1970), p. 434.
Schmidt-Kittler (1971), p. 49-50.
Type-species: Treposciurus mutabilis Schmidt- Kittler, 1970

4.1.3.1. **Treposciurus mutabilis helveticus** Schmidt-Kittler, 1971 (Plate VI, figs. 1-2)

Original reference: Schmidt-Kittler (1971), p. 53–57; figs. 23a-c, figs. 24a-e; plate 2, fig. 7.

Holotype: An isolated M_{1-2} (L.M. 40209).

Type-locality: Mormont-Eclépens (Switzerland).

Stratigraphic range on the Isle of Wight: Lower Headon Beds, Upper Headon Beds.

Material:
Headon Hill 1: 1 M_{1-2}, 2 M^{1-2}, 1 M^3.
Headon Hill 2: 1 D_4, 3 P_4, 7 M_{1-2}, 2 M_3, 1 D^4, 4 M^{1-2}, 1 M^3.
Totland Bay: 1 D_4, 1 P_4, 1 M_{1-2}, 1 D^4, 2 M^{1-2}, 1 M^3.
Headon Hill 3: 8 M_{1-2}, 2 M_3, 2 D^4, 3 P^4, 8 M^{1-2}, 3 M^3.
Headon Hill 4: 1 M_{1-2}, 1 M^3.
Headon Hill B: 1 D_4, 1 M_{1-2}, 1 D^4, 2 M^{1-2}.
Headon Hill C: 1 D_4, 1 M_{1-2}, 2 M^{1-2}.

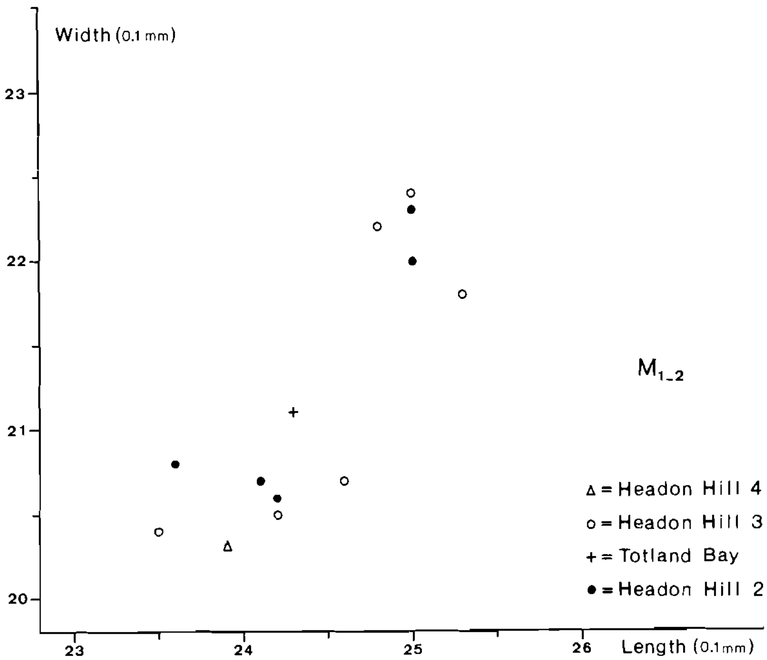
Measurements: see table V and text-figs. 22-23.

Description:
The dental pattern in *T. mutabilis helveticus* from the Isle of Wight closely fits the description of *T. mutabilis helveticus* from the type-locality (see Schmidt-Kittler, 1971). Therefore, only those features of the English material Schmidt-Kittler did not give in his description will be mentioned. Data on *T. mutabilis helveticus* are supplemented by the description of P_4 and D^4, which were unknown up to the present. Schmidt-Kittler's P_4 now appears to be a D_4.

	Locality	Length				Width		
		N	range	$\overline{X}$	s	N	range	$\overline{X}$
D_4	Totland Bay	1	–	22.6	–	1	–	16.7
P_4	Headon Hill 2	3	22.7 – 23.4	23.03	0.35	3	20.0 – 20.8	20.47
M_{1-2}	Headon Hill 4	1	–	23.9	–	1	–	20.3
	Headon Hill 3	8	23.5 – 26.4	24.75	0.87	6	20.4 – 22.4	21.33
	Totland Bay	1	–	24.3	–	1	–	21.1
	Headon Hill 2	5	23.6 – 25.0	24.38	0.61	5	20.6 – 22.3	21.28
M_3	Headon Hill 3	2	26.3 – 27.2	26.75	0.64	2	21.8 – 22.4	22.10
	Headon Hill 2	2	25.8 – 27.1	26.45	0.92	2	21.4 – 22.5	21.95
D^4	Headon Hill 3	2	22.5 – 22.9	22.70	0.28	2	19.5 – 19.8	19.65
	Totland Bay	1	–	22.5	–	1	–	21.9
P^4	Headon Hill 3	3	24.5 – 25.3	24.80	0.44	3	24.0 – 24.2	24.10
M^{1-2}	Headon Hill 3	7	22.5 – 23.5	23.04	0.40	8	21.8 – 24.9	23.93
	Totland Bay	2	22.8 – 23.7	23.25	0.64	2	25.9 – 26.9	26.40
	Headon Hill 2	1	–	23.0	–	1	–	25.6
	Headon Hill 1	2	21.4 – 22.4	21.90	0.71	2	20.5 – 22.0	21.25
M^3	Headon Hill 4	1	–	24.6	–	–	–	–
	Headon Hill 3	1	–	23.5	–	2	24.0 – 24.5	24.25
	Totland Bay	1	–	22.2	–	1	–	24.9
	Headon Hill 2	1	–	22.4	–	1	–	21.7
	Headon Hill 1	1	–	24.0	–	1	–	24.6

Table V. Measurements of the cheek teeth of *Treposciurus mutabilis helveticus* Schmidt-Kittler, 1971 (N = number of observations, $\overline{X}$ = mean value, s = standard deviation of the sample).

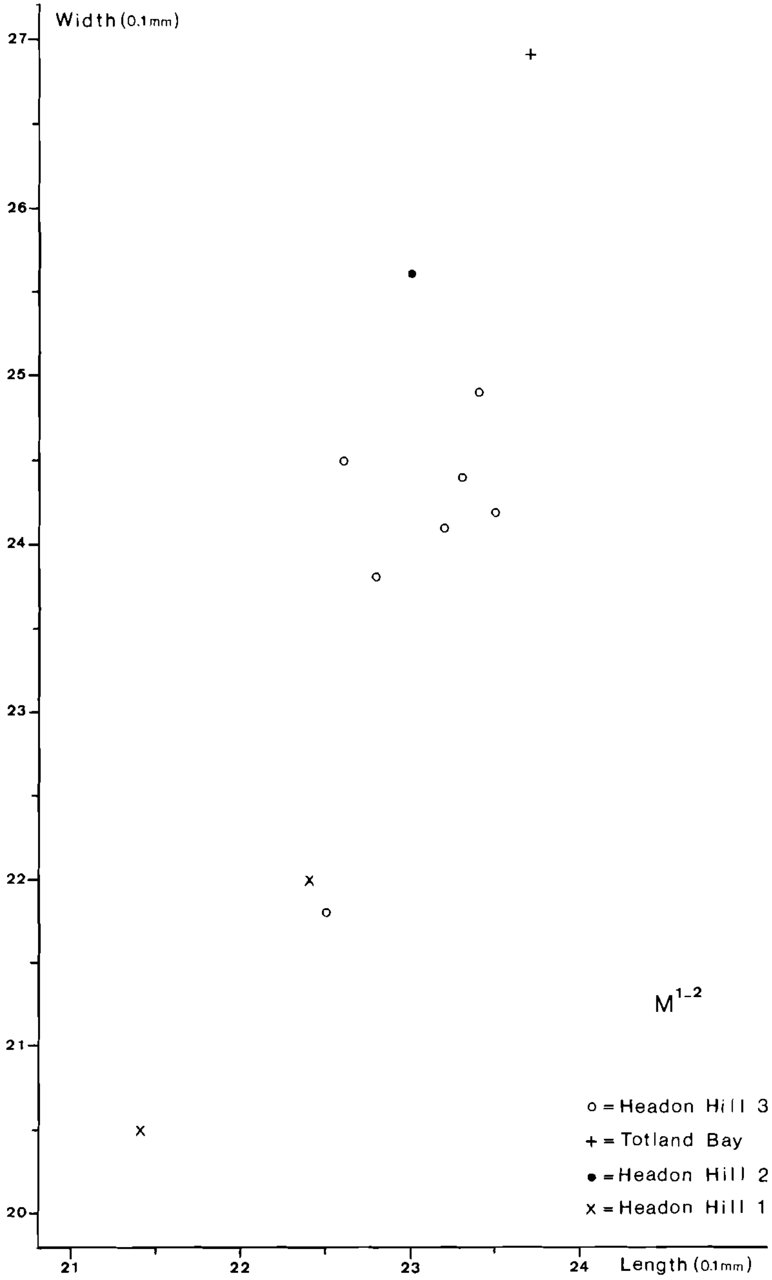
D_4: In two out of four specimens an anterolophid is present; this is connected to the protoconid as well as to the metaconid in one specimen, but only to the protoconid in the other. In the latter specimen the anterolophid is half as long as the distance between protoconid and metaconid. The protoconid and metaconid are connected by a metalophid; this may be very low at the lingual side of the protoconid. A small mesoconid, which is accompanied by a slight swelling on the buccal wall of the tooth, is present in two specimens. The enamel is rugose. In one specimen the ectolophid differs from the usual *Treposciurus* pattern in that it is directly connected to the hypoconid, not through the entolophid. The posterolophid may show a slight swelling at its buccal side.



Text-fig. 22 Scatter diagram showing length and width of the M_{1-2} of *Treposciurus mutabilis helveticus* Schmidt-Kittler, 1971.

P_4: The pattern of the premolar is similar to that of the molars. The anterior part of the tooth is relatively narrow. The metaconid, hypoconid and entoconid are well developed, while the protoconid is less prominent. The anterolophid, metalophid, entolophid, posterolophid and ectolophid are present in all specimens; in one specimen parts of the entolophid and the ectolophid are very low. The ectolophid is straight or S-shaped. The anterolophid is connected to the protoconid and the metaconid, and does not bear an anteroconid. The posterolophid may show a slight swelling at its buccal side. In two specimens the ectolophid is connected to the entolophid; this connection is clearly separated from the hypoconid (Plate VI, fig. 1). In another specimen the ectolophid and the entolophid reach the hypoconid at the same place. Neither a mesoconid nor a mesostylid are present. The enamel varies from reticulate to rugose, and is pitted rather deeply. The buccal wall of the tooth shows conspicuous vertical ridges. The occlusal surface is concave.

M_{1-2}, M_3: The anterolophid usually bears a low anteroconid, which is separated from the protoconid by a deep incision, but connected to the metalophid by a narrow crest. In occasional specimens the ectolophid and



Text-fig. 23 Scatter diagram showing length and width of the $M^{1\text{-}2}$ of *Treposciurus mutabilis helveticus* Schmidt-Kittler, 1971.

entolophid seem to reach the hypoconid at the same place. A mesoconid of variable size is present in most specimens. It is usually extended buccally by a vertical ridge, which divides the sinusid partly or completely into two parts. This ridge and the anterior part of the hypoconid may enclose a shallow depression. One or more additional vertical ridges are present on the buccal wall of some teeth. The posterolophid may show a slight swelling at the postero-lingual side of the hypoconid. Occasionally a mesostylid is present. Two specimens show a low ectostylid at the base of the sinusid. The ectolophid is always narrow at the anterior side of the mesoconid, and may even be interrupted.

D^4: The dental pattern of D^4 is similar to that of P^4 and M^{1-2}, apart from the prominent parastyle (Plate VI, fig. 2). D^4 are smaller than P^4. The protocone, paracone, hypocone and metacone are well developed; the protocone is somewhat lower than the other cusps. The protoconule is situated slightly anterior to the protoloph. A metaconule is present in three specimens. The anteroloph, posteroloph and endoloph are conspicuous crests. The sinus is wide and its buccal part is slightly directed forward. All specimens have a well-delimited mesostyle. The parastyle and paracone are separated by a deep incision. The anteroloph may show a cuspule at the lingual side of the parastyle. The enamel is strongly rugose.

P^4: The anteroloph is complete. The protocone, paracone, hypocone and metacone are all of about the same height. The endoloph is well developed, but in two specimens it is interrupted in the middle. All three P^4 show a protoconule; a protoloph is hardly developed. The hypocone and metacone are connected by a metaloph. A small but well-delimited mesostyle is present in one specimen. The two other specimens show a low longitudinal ridge instead of a mesostyle. The structure of the posteroloph is similar to that in M^{1-2}. The anteroloph and the paracone are connected. The enamel varies from reticulate to rugose, and is pitted rather deeply . The sinus does not extend far buccally.

M^{1-2}: The slight inward curves that are often present in the anteroloph and posteroloph and in the antero- and postero-lingual walls of the tooth are variable in shape and in size. Many specimens show a metaconule. The protoconule is absent in one specimen. The width and the buccal extent of the sinus are variable. The connection between the hypocone and the posteroloph is interrupted in two specimens. The anteroloph may bear a slight swelling at the antero-buccal side of the protocone.

M^3: A metacone is present in three out of five slightly worn specimens. In one of these the metacone and the posteroloph are connected, but in the two others the metacone and the posteroloph are separated by an incision.

In one specimen there is no connection between the protocone and protoconule. Occasional specimens show a low longitudinal ridge instead of a mesostyle.

Discussion:

Table V and text-figs. 22–23 show that the cheek teeth from Headon Hill 1, 2, 3 and 4 and Totland Bay do not differ systematically in length and width. Consistent differences in structure have not been observed either.

We refer our material to *T. mutabilis helveticus,* because it corresponds in its small size and dental pattern to this subspecies, rather than to *T. mutabilis mutabilis.* Yet it also shows features included in the diagnosis of *T. mutabilis mutabilis.* It cannot be ruled out that the differences Schmidt-Kittler (1971) recognized between the dental patterns of *T. mutabilis mutabilis* and *T. mutabilis helveticus* are mainly due to the limited number of specimens available from the type-localities of the two subspecies, Ehrenstein 1 (A) (Fed. Rep. Germany) and Mormont-Eclépens.

Schmidt-Kittler (1970, 1971) considered an ectolophid reaching the entolophid separate from the hypoconid of diagnostic value for *Treposciurus.* However, the assemblages from the Isle of Wight include teeth in which the ectolophid is directly connected to the hypoconid, not through the entolophid.

Remarks:

Besides from Germany, Switzerland and England, *Treposciurus mutabilis* has been recorded from Sosis (Spain), Le Bretou, Fons 4, Malpérié and Perrière (France) (Thaler, 1966; Hartenberger, 1973).

The D^4 (L.M. 40218) from Mormont-Eclépens, which Schmidt-Kittler (1971) described as *Pseudosciurus* A, belongs to *Treposciurus mutabilis.* The specimen may be attributed to *T. mutabilis helveticus* because of its provenance.

4.1.3.2. **Treposciurus intermedius** (Schlosser, 1884) (Plate VI, figs. 3–10)

Original reference: Sciuroides intermedius Schlosser (1884); p. 62–63; plate I, figs. 9, 11, 13 and 22.

Emended diagnosis:

Metalophule I partly or completely present. Protoloph and metaloph well developed. Metaconule usually absent.

Lectotype (designated by Dehm, 1937): A lower jaw with D_4–M_3 (B.S.P.G. 1879 XV-192).

Type-locality: Escamps (near Lalbenque, Lot, France), as understood in old collections.

Stratigraphic range on the Isle of Wight: Lower Headon Beds, Upper Headon Beds, Bembridge Marls.

Material:
Headon Hill 1: 2 M^{1-2}, 1 M^3.
Headon Hill 2: 1 M_3.
Headon Hill C: 1 P^4.
Whitecliff Bay 2A: 1 D^4, 1 P^4, 3 M^{1-2}, 1 M^3, 1 D_4?
In addition there are fragments of upper cheek teeth from Headon Hill 1 and 4.

Measurements: see table VI.

Description:
M_3: The dental structure is identical to that of M_3 in *T. intermedius* from the type-locality. The metalophid shows an incision in the middle.
D^4: The tooth is relatively low crowned. The four main cusps are well developed. The hypocone and paracone are slightly higher than the protocone and metacone. The protoloph and metaloph are complete. The protoloph bears a prominent protoconule. The anteroloph and posteroloph are low. They are connected with the protocone and paracone, and with the hypocone and metacone, respectively. The buccal part of the anteroloph is protuberant. The mesostyle is well delimited. A short crest, which represents

	Locality	Length			Width		
		N	range	$\bar{X}$	N	range	$\bar{X}$
M_3	Headon Hill 2	1	–	20.0	1	–	15.8
D^4	Whitecliff Bay 2A	1	–	19.0	1	–	17.5
P^4	Whitecliff Bay 2A	1	–	21.2	1	–	19.8
M^{1-2}	Whitecliff Bay 2A	3	18.6–20.2	19.60	3	18.1–21.3	20.20
	Headon Hill 1	2	18.2–18.4	18.30	2	18.6–18.9	18.75
M^3	Whitecliff Bay 2A	1	–	19.6	1	–	19.9
D_4	Whitecliff Bay 2A	1	–	16.8	1	–	13.1

Table VI. Measurements of the cheek teeth of *Treposciurus intermedius* (Schlosser, 1884) (N = number of observations, $\bar{X}$ = mean value).

the lingual part of the metalophule I, extends from the endoloph into the central basin of the tooth. The buccal part of the sinus is slightly directed forward. The endoloph is very low in the middle. The enamel is rugose.

P^4: The dental pattern in one of the two P^4 available (Plate VI, fig. 5) closely resembles that in M^{1-2}; the tooth differs from the molars in that it is slightly enlarged antero-buccally. The protoconule is isolated from the protocone and paracone by incisions. The metaloph is constricted just buccal to the hypocone. The mesostyle is well delimited. The buccal part of the metalophule I is absent. The connection between the endoloph and metalophule I is indistinct.

The occlusal pattern in the other P^4 (Plate VI, fig. 6) is rather different from that in M^{1-2}. The four main cusps are voluminous. The protoloph and metaloph are complete. The tooth is enlarged antero-buccally. The paracone and metacone are connected by a crest as high as the anteroloph and posteroloph; this crest bears an indistinct mesostyle. The buccal part of the sinus is slightly directed forward. The endoloph is interrupted just posterior to the protocone. The enamel is strongly rugose.

M^{1-2}: The occlusal surfaces of the M^{1-2} from Headon Hill are square (Plate VI, fig. 7), while the M^{1-2} from Whitecliff Bay 2A are anteriorly much wider than posteriorly (Plate VI, figs. 8-9). This indicates that they are respectively M^1 and M^2. The four main cusps are well developed. The paracone is the highest cusp. The protoloph and metaloph are complete. The protoconule may be prominent or indistinct. In one specimen the metaloph bears a weak metaconule. In another specimen the metaloph is constricted just buccal to the hypocone. The low anteroloph and posteroloph are connected with the protocone and paracone, and with the hypocone and metacone, respectively. The mesostyle is usually well delimited; only in one specimen it is connected with the paracone. In most specimens the more or less incomplete metalophule I is connected to the endoloph, near the hypocone; in one specimen it is directly connected to the hypocone. In some M^{1-2} the posteroloph shows a swelling at the postero-buccal side of the hypocone. The buccal part of the sinus is slightly directed forward. The endoloph is low in the middle. The enamel is rugose.

M^3: The posterior part of the tooth is rounded. The protocone and paracone are well developed, the hypocone and metacone are indistinct. The protoloph and metaloph are complete. The protoloph bears a small protoconule. The anteroloph is low, the posteroloph is nearly as high as the protoloph and metaloph. The anteroloph and posteroloph are connected with the protocone and paracone, and with the hypocone and metacone, respectively. The mesostyle has the shape of a crest and is connected with the metacone. The sinus extends only slightly buccally. The enamel is rugose.

D_4 ?: The specimen is rather worn, which prevents the observation of details of the occlusal pattern. The metaconid, hypoconid and entoconid are prominent, the protoconid is low. The metalophid and entolophid are well developed. The anterolophid is absent. The posterolophid is lower than the metalophid and entolophid, and is connected with the hypoconid and entoconid. The ectolophid seems to be connected to the hypoconid and bears an indistinct mesoconid.

Discussion:

The material from Escamps on which Schlosser (1884) based his *Sciuroides intermedius* consists of two lower jaws with $D_4/P_4 - M_3$ (one of which was later designated as the lectotype) and one upper jaw with $P^4 - M^3$ (B.S.P.G. 1879 XV – 543) (Schlosser, 1884; Dehm, 1937).

Material of *Treposciurus intermedius* from the Isle of Wight includes only one lower tooth with certainty, a M_3, which is identical to the M_3 in the two lower jaws from Escamps. Unfortunately this tooth is rather uncharacteristic, which means that the classification of our material has to be based on the upper teeth mainly. Indeed these teeth show close similarity to the $P^4 - M^3$ in the upper jaw B.S.P.G. 1879 XV – 543, although the specimens from the Lower and Upper Headon Beds are slightly smaller.

The determination is complicated by the fact that Schmidt-Kittler (1971) excluded B.S.P.G. 1879 XV – 543 from *Treposciurus intermedius*. He was of the opinion that the teeth in the upper jaw L.P.M. UM 1830 from Quercy (Thaler (1966), p. 36; plate I, fig. C; fig. 6C) are structurally better in harmony with the lower teeth of *T. intermedius*. In addition, he considered the forward position of the posterior border of the incisive foramen in L.P.M. UM 1830 well-suited to *Treposciurus*.

In our opinion, there is no good reason to exclude B.S.P.G. 1879 XV – 543, and consequently our material, from *T. intermedius;* the more so, because the cheek teeth in B.S.P.G. 1879 XV – 543 are rather worn and the posterior border of the incisive foramen is damaged. Adequate quantities of upper and lower cheek teeth from one locality are necessary to answer this question conclusively.

The single P^4 from Headon Hill C is distinctly smaller than the one from Whitecliff Bay 2A. The M^{1-2} from Headon Hill 1 are also smaller than those from Whitecliff Bay 2A. More material may show significant differences in size between assemblages from the Lower and Upper Headon Beds on the one hand and assemblages from the Bembridge Marls on the other.

Remark:

The material from Fons 4 (France) Hartenberger (1973) described as *Suevosciurus (Microsuevosciurus)* aff. *minimus* is very similar in dental pattern to *T. intermedius,* but it is of a somewhat smaller size. In our opinion, it should not be referred to *Suevosciurus minimus.*

4.1.4. Genus **Paradelomys** Thaler, 1966

Original reference: Thaler (1966), p.39.
Type-species: Adelomys (Paradelomys) crusafonti Thaler, 1966.
Other species referred to Paradelomys:
Sciuroides quercyi Schlosser, 1884,
Adelomys depereti Stehlin and Schaub, 1951,
Paradelomys spelaeus Hartenberger, 1973.

Emended diagnosis:

Main cusps prominent. Metalophid, entolophid, ectolophid and anteroconid or anterolophid conspicuous. Junction of ectolophid and entolophid at some distance from the hypoconid. Buccal part of the sinus distinctly directed forward. Protoconule usually well developed. Mesoloph often present.

Differential diagnosis:

The cheek teeth of *Paradelomys* differ from those of *Pseudosciurus* in the more conspicuous crests, in the more circular cusps, in the relatively smooth enamel. The P^4 of *Paradelomys* do not show a parastyle.

Discussion:

In previous studies (Thaler, 1966; Hartenberger, 1969 and 1973; Schmidt-Kittler, 1971) the (sub)genera *Paradelomys* and *Adelomys* comprised the pseudosciurid species in which the upper cheek teeth show a sinus distinctly directed forward, and the lower cheek teeth show a conspicuous metalophid, entolophid, ectolophid and anteroconid or anterolophid. Thaler created *Paradelomys* as a subgenus of *Adelomys,* to include *A.(P.) crusafonti* and a number of specimens from Quercy (France) that he did not name specifically. His subgenus *Adelomys* comprised *A.(A.) depereti* and the forms from Mormont-Entreroches (Switzerland) and Quercy that Stehlin and Schaub (1951) had described and figured under the name *Adelomys vaillanti* Gervais, 1848–1852.

Hartenberger (1969) elevated *Paradelomys* to generic level, which was adopted by Schmidt-Kittler. The latter author observed that *Sciuroides quercyi* belongs to *Paradelomys.*

Hartenberger (1973) subsequently emended the diagnosis of *Paradelomys,* while he suppressed *Adelomys* for lack of data on the type-species, *A. vaillanti.* He added a new species to *Paradelomys,* i.e. *P. spelaeus.*

Schmidt-Kittler likewise repudiated Thaler's diagnoses; he distinguished between *Paradelomys* and *Adelomys* by the absence or presence of a connection between the metaconule and the posteroloph. However, in the assemblage of *P. spelaeus* from Escamps (France) stored in the Geologisch Instituut at Utrecht both morphotypes are present, although most upper teeth show the connection between metaconule and posteroloph. Consequently this difference is not of diagnostic value and all species that were up to this time considered to belong to either *Paradelomys* or *Adelomys* should be grouped in one genus. It is preferable to follow Hartenberger's proposal to suppress the genus *Adelomys,* because of the uncertainty with regard to the nature of *A. vaillanti.*

Adelomys depereti was first described from Euzet (France) on one lower jaw with P_4–M_2. Hartenberger (1973) collected abundant material of the same species from Fons 4, Malpérié and Perrière (France). He referred this to *Sciuroides intermedius* Schlosser, 1884 and consequently considered *Adelomys depereti* to be synonymous with *Sciuroides intermedius. Adelomys depereti,* however, is a separate species of the genus *Paradelomys.*

In the past the position of the posterior border of the incisive foramen has been used as a diagnostic character of *Paradelomys* (Thaler, 1966; Hartenberger, 1973). In the few available (fragments of) palates of *Paradelomys,* this position shows, however, considerable variation. According to Thaler the posterior border of the incisive foramen does not reach backward to the anterior side of the P^4 in the upper jaw L.P.M. MM 718 from Quercy (Thaler (1966), p. 42; plate II, fig. A), which he classified as *Adelomys (Paradelomys)* sp.; Schmidt-Kittler observed that the posterior border of the incisive foramen in this specimen is in line with the anterior side of the zygomatic arch. Thaler considered the structure of the palate in L.P.M. MM 716 from Quercy (Thaler (1966), p. 43), which he also referred to as *Adelomys (Paradelomys)* sp., to be of his type AB. He did not describe this type, but it probably shows the posterior border of the incisive foramen to be in line with (the anterior side of) the zygomatic arch. A skull of *Paradelomys* sp. from Quercy, described by Hartenberger (1973, p. 27–29; text-fig. 7; plate VII, fig. 4), shows the incisive foramina reaching backward to the middle of the zygomatic arch. In contrast to these specimens, the upper jaw of *Paradelomys quercyi* (B.S.P.G. 1879 XV – 541) (Plate III, fig. 12) from Escamps (Quercy), which was previously figured and described by Schlosser (1884, p. 60; plate I, fig. 10) and Dehm (1937, p. 282; plate XV, fig. 1), clearly shows the incisive foramen reaching backward to the anterior side of the P^4. In our opinion, the variable position of the incisive foramen prevents a definite conclusion on the palatal structure in *Paradelomys.*

4.1.4.1. **Paradelomys quercyi** (Schlosser, 1884)

Original reference: Sciuroides quercyi Schlosser, 1884; p. 60–62; plate I, figs. 1–5, 7, 8, 10, 17, 23, 24 and 31.

Diagnosis:
Anteroconid connected with the metalophid by a short longitudinal crest in M_1–M_3. Metalophule I usually present.

Differential diagnosis:
P. quercyi differs from *P. crusafonti* in its considerably larger-sized cheek teeth, in the presence of an anteroconid in M_1–M_3, in the distinct protoconid and metaconid in P_4 and in the presence of a metalophule I in most upper cheek teeth.
P. quercyi differs from *P. depereti* in its considerably larger-sized and lower-crowned cheek teeth, in the invariable presence of an endoloph and in the better delimited protoconule.
P. quercyi differs from *P. spelaeus* in the presence of a metalophule I in most upper cheek teeth, in the usual absence of a connection between the metaconule and the posteroloph, and in the better delimited protoconule.

Lectotype (designated by Dehm, 1937): A lower jaw with P_4–M_3 (B.S.P.G. 1879 XV – 191).

Type-locality: Escamps (near Lalbenque, Lot, France), as understood in old collections.

Paradelomys quercyi quercyi (Schlosser, 1884) (Plate VII, figs. 1-2, 4–7, 9–10)

Diagnosis: Mean length $M^{1-2} > 2.40$ mm.

Stratigraphic range on the Isle of Wight: Upper Headon Beds.

Material:
Headon Hill 3: 2 P_4, 5 M_{1-2}, 1 M_3, 3 D^4, 1 P^4, 10 M^{1-2}, 5 M^3.
Headon Hill 4: 3 D_4, 4 M_{1-2}, 1 M_3, 5 M^{1-2}.
Headon Hill A: 1 P_4.

4.1.4.2. **Paradelomys quercyi vectisensis** n. subsp. (Plate VII, figs. 3 and 8)

Diagnosis: Mean length $M^{1-2} < 2.40$ mm.

Derivatio nominis: After the Roman name of the Isle of Wight, Vectis.

Holotype: An isolated M^{1-2} (G.I.U. HH2 1221) (Plate VII, fig. 8).

Measurements holotype: 22.6 x 24.6.

Type-locality: Headon Hill 2 (Isle of Wight, England).

Paratypes: 5 M_{1-2} (HH2 1181–1185); 1 M_3 (HH2 1191); 2 D^4 (HH2 1201–1202); 4 M^{1-2} (HH2 1222–1225); 3 M^3 (HH2 1231–1233).

Stratigraphic range: Lower Headon Beds.

Further material: Totland Bay: 1 P_4.

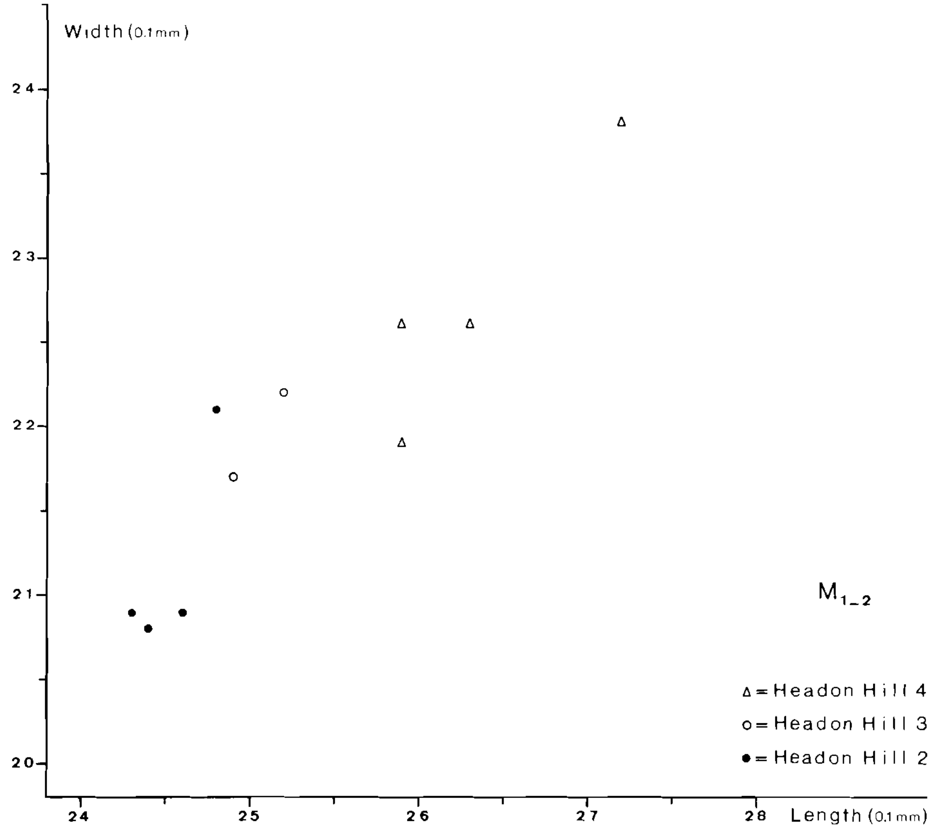
Measurements of P. quercyi quercyi and P. quercyi vectisensis: see table VII and text-figs. 24–25.

Description of P. quercyi quercyi and P. quercyi vectisensis:

D_4: In the only complete D_4 (Plate VII, fig. 2) the four main cusps are

	Locality	Length				Width		
		N	range	$\bar{X}$	s	N	range	$\bar{X}$
D_4	Headon Hill 4	1	–	22.4	–	1	–	16.4
P_4	Headon Hill 3	1	–	26.7	–	1	–	23.3
M_{1-2}	Headon Hill 4	4	25.9–27.2	26.33	0.61	4	21.9–23.8	22.73
	Headon Hill 3	4	24.9–27.4	25.90	1.12	2	21.7–22.2	21.95
	Headon Hill 2	4	24.3–24.8	24.53	0.22	5	20.0–22.1	20.94
M_3	Headon Hill 4	1	–	30.1	–	1	–	22.6
	Headon Hill 3	1	–	30.5	–	1	–	22.0
D^4	Headon Hill 3	2	21.8–22.7	22.25	0.64	2	20.9–21.2	21.05
	Headon Hill 2	1	–	18.7	–	1	–	16.9
P^4	Headon Hill 3	1	–	22.9	–	1	–	22.8
M^{1-2}	Headon Hill 4	5	24.3–26.1	25.46	0.74	4	26.5–28.7	27.55
	Headon Hill 3	9	23.0–25.2	24.21	0.69	6	23.7–26.4	25.37
	Headon Hill 2	5	22.5–23.3	22.76	0.31	3	24.4–24.9	24.63
M^3	Headon Hill 3	4	24.7–26.4	25.55	0.70	3	24.6–26.0	25.47
	Headon Hill 2	1	–	20.8	–	2	21.6–22.3	21.95

Table VII. Measurements of the cheek teeth of *Paradelomys quercyi quercyi* (Schlosser, 1884) and *Paradelomys quercyi vectisensis* n. subsp. (N = number of observations, $\bar{X}$ = mean value, s = standard deviation of the sample).

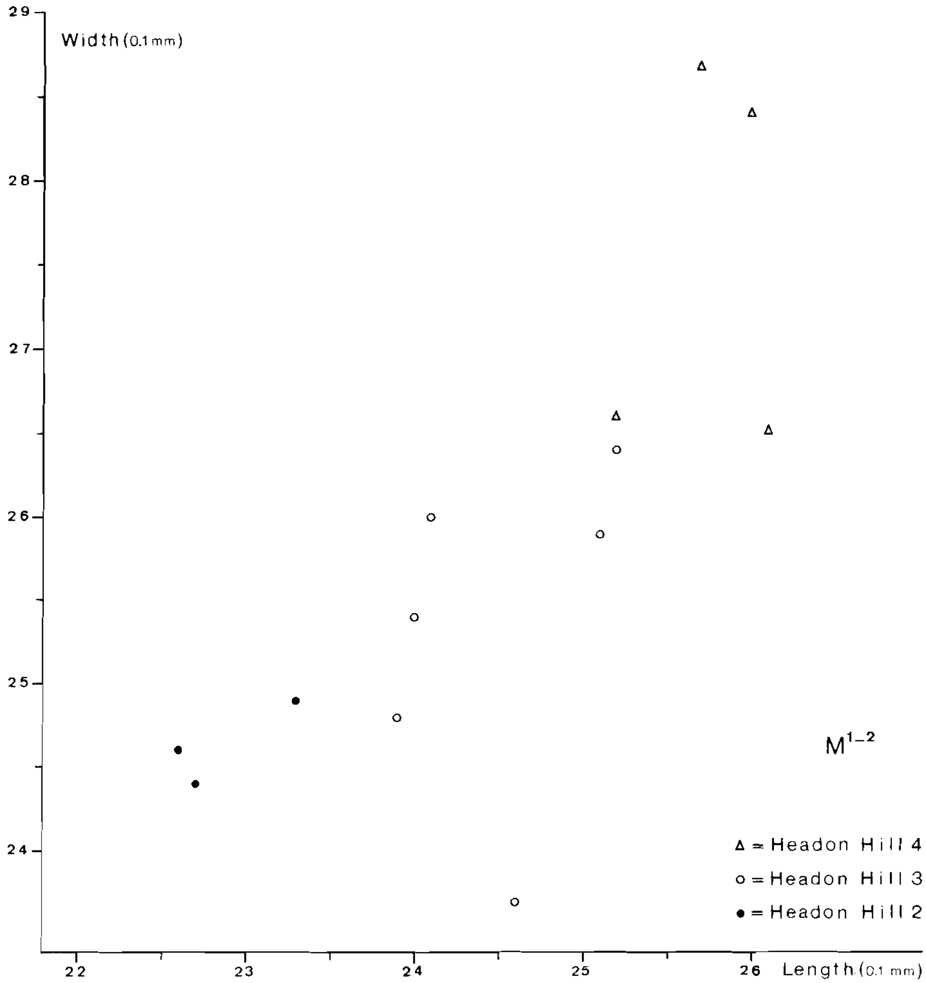


Text-fig. 24 Scatter diagram showing length and width of the M_{1-2} of *Paradelomys quercyi quercyi* (Schlosser, 1884) and *Paradelomys quercyi vectisensis* n.subsp.

high and pointed. The protoconid is somewhat lower than the other cusps. The entolophid is the highest crest, the ectolophid and posterolophid are lower. There is some distance between the hypoconid and the junction of the ectolophid and the entolophid. The protoconid and metaconid are situated close together, but are separated by an incision. The mesostylid is small. In one specimen the ectolophid bears a weak mesoconid. Slight irregularities are present within the central valley.

P_4: The four main cusps are prominent. The ectolophid and posterolophid are lower than the strongly developed entolophid. In three specimens there is some distance between the hypoconid and the junction of the ectolophid and the entolophid (Plate VII, fig. 1), while in the fourth specimen the ectolophid and entolophid are connected at the lingual wall of the hypoconid. The protoconid and metaconid may be connected by a metalophid, or they may be separated by an incision. All specimens show a mesoconid. The posterolophid bears an indistinct hypoconulid in one specimen. The enamel is slightly rugose.

M_{1-2}, M_3: The four main cusps are prominent. The metaconid and entoconid are the highest cusps. The metalophid, entolophid, ectolophid and posterolophid are distinct. The ectolophid and posterolophid are somewhat lower than the other crests. There is some distance between the hypoconid and the junction of the ectolophid and the entolophid.The metalophid often



Text-fig. 25 Scatter diagram showing length and width of the M^{1-2} of *Paradelomys quercyi quercyi* (Schlosser, 1884) and *Paradelomys quercyi vectisensis* n.subsp.

shows a slight incision in the middle. A distinct anteroconid is present, which is usually connected with the metalophid by a short longitudinal crest, forming an antesinusid. The ectolophid often bears a mesoconid. In two specimens the mesoconid is enlarged buccally to a vertical crest, which divides the sinusid into two parts. In one M_3 (Plate VII, fig. 5) a mesostylid is present. The enamel is smooth or slightly rugose.

D^4: The four main cusps are prominent. The anteroloph bears a parastyle, which is separated from the paracone by an incision. The protoconule is well delimited and is situated anterior to the protoloph. The metaconule is more or less incorporated in the metaloph. The metaloph is usually complete; in one specimen the part between the metaconule and the hypocone is absent. The low anteroloph and posteroloph are connected with the protocone and parastyle, and with the hypocone and metacone, respectively. The sinus is bordered by the endoloph and the lingual part of the protoloph. Either a prominent mesostyle or a short mesoloph is present. A distinct metalophule I extends between the endoloph and the metacone. The junction of metalophule I and endoloph is situated near the hypocone. The enamel is slightly rugose.

P^4: The only P^4 attributed to *P. quercyi* (Plate VII, fig. 6) is rather different from the M^1–M^3 (cf. Discussion). The four main cusps are voluminous, but truncated. The protoconule is absent, although a slight swelling of the anteroloph may represent this cusp. An indistinct crest is present between this swelling and the protocone. The metaloph consists of two cusps, the buccal one of which is connected with the metacone and the lingual one with the posteroloph. The posteroloph is low and connected with the metacone. The sinus is mainly bordered by the endoloph. The endoloph connects the hypocone and the anteroloph. A large mesostyle is present. The metalophule I is conspicuous. A crest, which is of the same height as the metalophule I and the endoloph, extends between the paracone and the endoloph. Its connection with the endoloph is situated anterior to the connection between metalophule I and endoloph. The enamel shows some additional cusps and crests.

M^{1-2}: The four main cusps are prominent. The paracone and metacone are the highest cusps. The protoconule is well delimited and is situated anteriorly against the protoloph. The metaconule is large. It is elongated lingual-buccally, connecting the hypocone and the metacone in all specimens from Headon Hill 2, in three specimens from Headon Hill 3 and in one specimen from Headon Hill 4 (Plate VII, fig. 9). In the other M^{1-2} there is no connection between the metaconule and the hypocone, but often an indistinct connection between the metaconule and the posteroloph. The low anteroloph is connected with the protocone, but separated from the paracone by an incision. The posteroloph is also low, and connected with the hypocone and the metacone in all but one specimen. The sinus is bordered by the endoloph and the lingual part of the protoloph. Most specimens show a mesoloph of variable length, instead of a mesostyle. The metalophule I is distinct, but in some specimens it is incomplete. The enamel is slightly rugose.

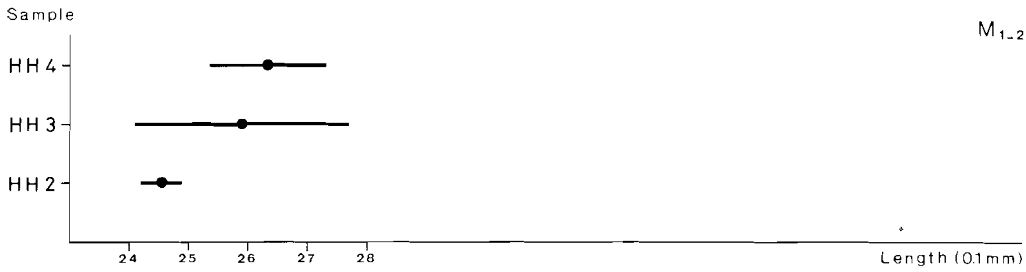
M^3: The posterior part of the M^3 is rounded, the hypocone and metacone are indistinct. The paracone is very high. The protoconule is usually well delimited and is situated anteriorly against the protoloph. In one specimen (Plate VII, fig. 10) the protoloph is interrupted just buccal to the protoconule. Within the posterior valley irregular crests of variable length and direction are present. Parts of these are probably homologous with parts of the metaloph and mesoloph. The anteroloph is connected with the protocone, and separated from the paracone by an incision. The posteroloph shows incisions buccally. The sinus is bordered by the endoloph and the lingual part of the protoloph. The enamel is rugose, especially in the specimens from Headon Hill 3.

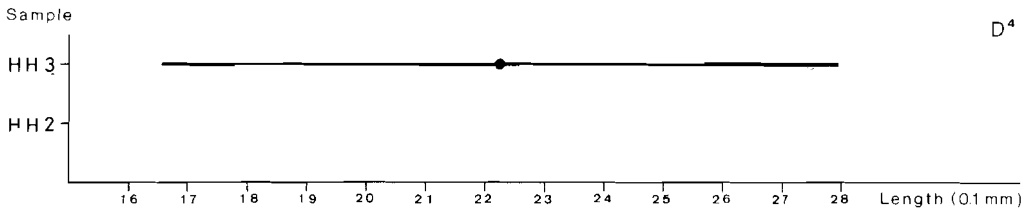
Comparison of the lengths of the cheek teeth:

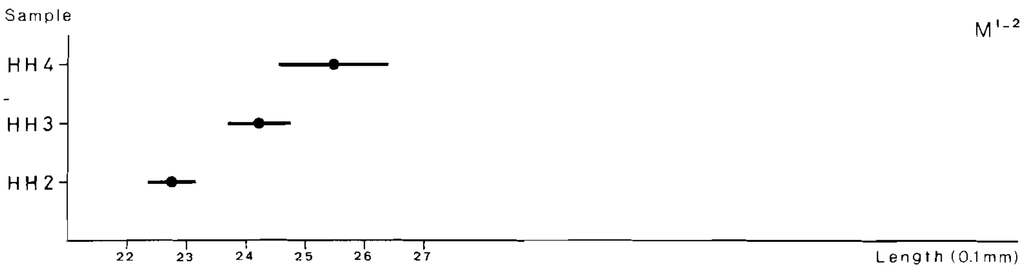
Table VII and text-figs. 24–25 show that the cheek teeth of *P. quercyi* increase in length and width in the successive levels Headon Hill 2, 3 and 4. Only the single M_3 from Headon Hill 4 is slightly shorter than the single M_3 from Headon Hill 3. Whether the increase in length is significant has been

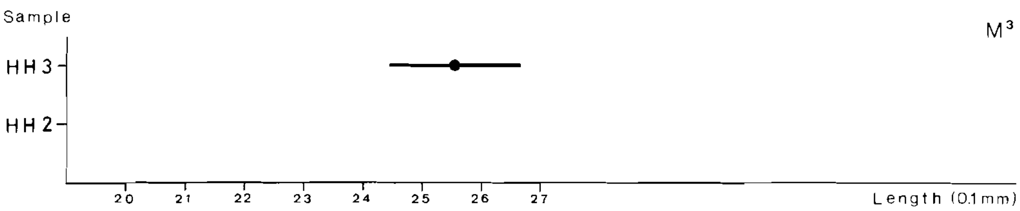
	Locality	N	$\overline{X}$	confidence interval
M_{1-2}	Headon Hill 4	4	26.33	$25.36 < \mu < 27.30$
	Headon Hill 3	4	25.90	$24.12 < \mu < 27.68$
	Headon Hill 2	4	24.53	$24.18 < \mu < 24.88$
D^4	Headon Hill 3	2	22.25	$16.53 < \mu < 27.97$
	Headon Hill 2	1	18.7	–
M^{1-2}	Headon Hill 4	5	25.46	$24.54 < \mu < 26.38$
	Headon Hill 3	9	24.21	$23.68 < \mu < 24.74$
	Headon Hill 2	5	22.76	$22.37 < \mu < 23.15$
M^3	Headon Hill 3	4	25.55	$24.44 < \mu < 26.66$
	Headon Hill 2	1	20.8	–

Table VIII. Confidence intervals for estimating the mean value of the length of cheek teeth of *Paradelomys quercyi quercyi* (Schlosser, 1884) and *Paradelomys quercyi vectisensis* n. subsp. (N = number of observations, $\overline{X}$ = mean value).









Text-figs. 26–29 Confidence intervals for estimating the mean length of M_{1-2}, D^4, M^{1-2} and M^3 of *Paradelomys quercyi quercyi* (Schlosser, 1884) and *Paradelomys quercyi vectisensis* n.subsp.

studied by the determination of confidence intervals for estimating the population means, and by testing the differences in sample mean with the statistic t. Confidence intervals are given in table VIII and are represented graphically in text-figs. 26–29. Table and figures also include a (mean) value when only one observation is available. Values of t are given in table IX.

Apparently, there is a significant increase in length of M^{1-2} and M^3 between Headon Hill 2 and 3; of M_{1-2} and M^{1-2} between Headon Hill 2 and 4; of M^{1-2} between Headon Hill 3 and 4.

	M_{1-2}	D^4	M^{1-2}	M^3
HH3–HH4	0.672(6)	–	*3.174*(12)	–
HH2–HH4	*5.522*(6)	–	*7.541*(8)	–
HH2–HH3	2.395(4.31)	4.555(1)	*4.394*(12)	*6.111*(3)

Table IX. t values for comparison of the mean length of the cheek teeth of *Paradelomys quercyi quercyi* (Schlosser, 1884) and *Paradelcmys quercyi vectisensis* n. subsp. (Numbers of degrees of freedom in parentheses; significant values of t in italics).

Discussion:

The assemblages from Headon Hill 2, 3 and 4 seem to represent a chronocline, showing a gradual increase in size. Between the ends of the chronocline the increase in length is significant, which warrants the distinction of subspecific categories. As not all teeth show a significant increase in length between Headon Hill 2 and 3, and between Headon Hill 3 and 4, only two subspecies are recognized. The smaller one is present in Headon Hill 2 and the larger one in Headon Hill 4. The mean length of M^{1-2} is applied as a diagnostic character. The limit between the two subspecies is fixed arbitrarily at a mean length of 24.0 (= 2.40 mm). With such a definition, the assemblage of Headon Hill 3 cannot be placed with certainty (cf. table VIII). It might be referred to as *P. quercyi* ex. interc. *quercyi-vectisensis.*

The material of *P. quercyi* from Escamps stored in the Bayerische Staatssammlung für Paläontologie und historische Geologie corresponds better in size with the material from Headon Hill 3 and 4 than with the material from Headon Hill 2. The length and width of the single M^1 from Escamps (in a fragment of a right upper jaw with P^4 and M^1, B.S.P.G. 1879 XV-541) (Plate III, fig. 12) amount to 24.8 and 23.7 respectively. Probably the assemblage of *P. quercyi* from Escamps belongs to the larger subspecies, which is consequently the nominate one.

No structural differences have been observed between the three assemblages from the Isle of Wight, nor between the lower teeth from Escamps and the lower teeth from the Isle of Wight. The M^1 in B.S.P.G. 1879 XV – 541, however, differs slightly from the M^{1-2} from the Isle of Wight, while the P^4 in B.S.P.G. 1879 XV – 541 and the single P^4 from the Isle of Wight show considerable differences. In the M^1 from Escamps the metalophule I is relatively low and connected with the metaconule. The metaconule and the hypocone are isolated cusps. In the P^4 from Escamps the protoconule is absent. The metaloph is low, but complete. The mesoloph is well developed and connected with the endoloph. Yet the structure of this P^4 is very similar to that of the M^{1-2}, which indicates that the P^4 from the Isle of Wight is an aberrant specimen; it has been assigned to *P. quercyi* because of its distinctly forward directed sinus, its prominent cusps and crests, and because of the absence of a parastyle.

4.2. Family THERIDOMYIDAE Alston, 1876

Introduction.

The collections from the mammal-yielding localities of the Isle of Wight are all dominated by theridomyid teeth. These teeth are assigned to three genera, *Isoptychus* Pomel, 1853, *Pseudoltinomys* Lavocat, 1951 and *Ectropomys* Bosma and Schmidt-Kittler, 1972, which genera belong to three different subfamilies, the Theridomyinae, Issiodoromyinae Lavocat, 1951 and Oltinomyinae Hartenberger, 1971. Representatives of the fourth theridomyid subfamily, the Columbomyinae Thaler, 1966, have not been obtained from the Isle of Wight.

Specimens of *Isoptychus* occur in abundance. The section below is devoted to the disentanglement of their complicated patterns of variation.

4.2.1. Analysis of the taxonomic and phylogenetic relations between the Isoptychus assemblages from the Isle of Wight.

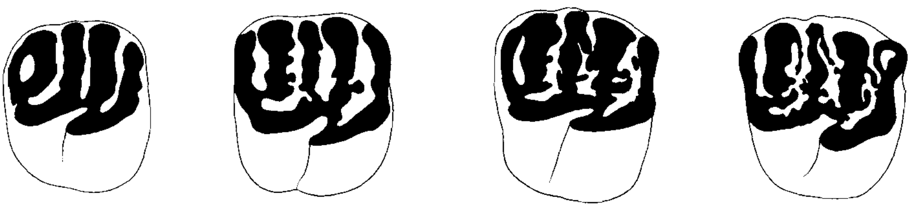
Introduction.

Examination of the cheek teeth of the genus *Isoptychus* has revealed considerable variation in their dimensions, in the absence or presence of small accessory cusps and crests, and in the structure of the metalophid. It will be attempted to express this variation in the taxonomy, and to determine the significance of differences between assemblages from successive stratigraphic levels. First, the assemblages from the Headon Hill-Bouldnor Cliff section will be compared in detail. Next, these assemblages will be compared with the remaining assemblages.

4.2.1.1. Methods of comparison.

The parameters applied in comparing the *Isoptychus* assemblages are the length of the M_{1-2} and M^{1-2} (the most abundant elements), the degree of complexity of the dental pattern and the type of metalophid.

The dental pattern is more or less complex because of the presence or absence of accessory cuspules and crests. These vary much in form and in number and persist until a late stage of wear. The variation in the prominence of these features makes it impossible to enumerate them according to a consistent technique, and as a result it has been thought more useful to express the variety by means of a simple scale in which four degrees of complexity – conveniently specified as *simple, slightly complex, moderately complex* and *very complex* – are recognized. Text-fig. 30 reflects what is meant by these terms. The degree of complexity has only been determined in the M^{1-2}. We could not always exclude some influence of the stage of wear upon our designation.



1 2 3 4

Text-fig. 30 M^{1-2} of *Isoptychus headonensis* n.sp., showing the four degrees of complexity of the dental pattern (1 = simple, 2 = slightly complex, 3 = moderately complex, 4 = very complex).

The metalophid in the M_1, M_2 and M_3 may be one single crest or it may be double, consisting of an anterior and a posterior branch. If two branches are present, the anterior one is always complete, while the posterior one is either incomplete or complete, in the latter case extending to the protoconid and the metaconid. The anterior and posterior branches of the metalophid are connected at the protoconid and/or the metaconid; extra connections are usually present in between these cusps. The posterior side of the anterior branch and the anterior and posterior sides of the posterior branch may bear small cusps and crests.

Three types of metalophid have been distinguished:

– a *simple metalophid* (Plate I, fig. 6): The metalophid is one single crest. It may show an antero-buccal inward fold, which is occasionally closed. This small fold is sometimes accompanied by an anterior accessory cuspule of variable size.

– a *metalophid of intermediate type* (Plate I, fig. 3): The metalophid is double; the total extent of the posterior branch is half or less than half of the distance between protoconid and metaconid.

– a *complex metalophid* (Plate I, figs. 4 and 5): The metalophid is double; the total extent of the posterior branch is more than half of the distance between protoconid and metaconid.

Molars in jaw fragments from various localities in the Hampshire Basin show that the structure of the metalophid in the M_1, M_2 and M_3 of single individuals is of the same type or of different types:

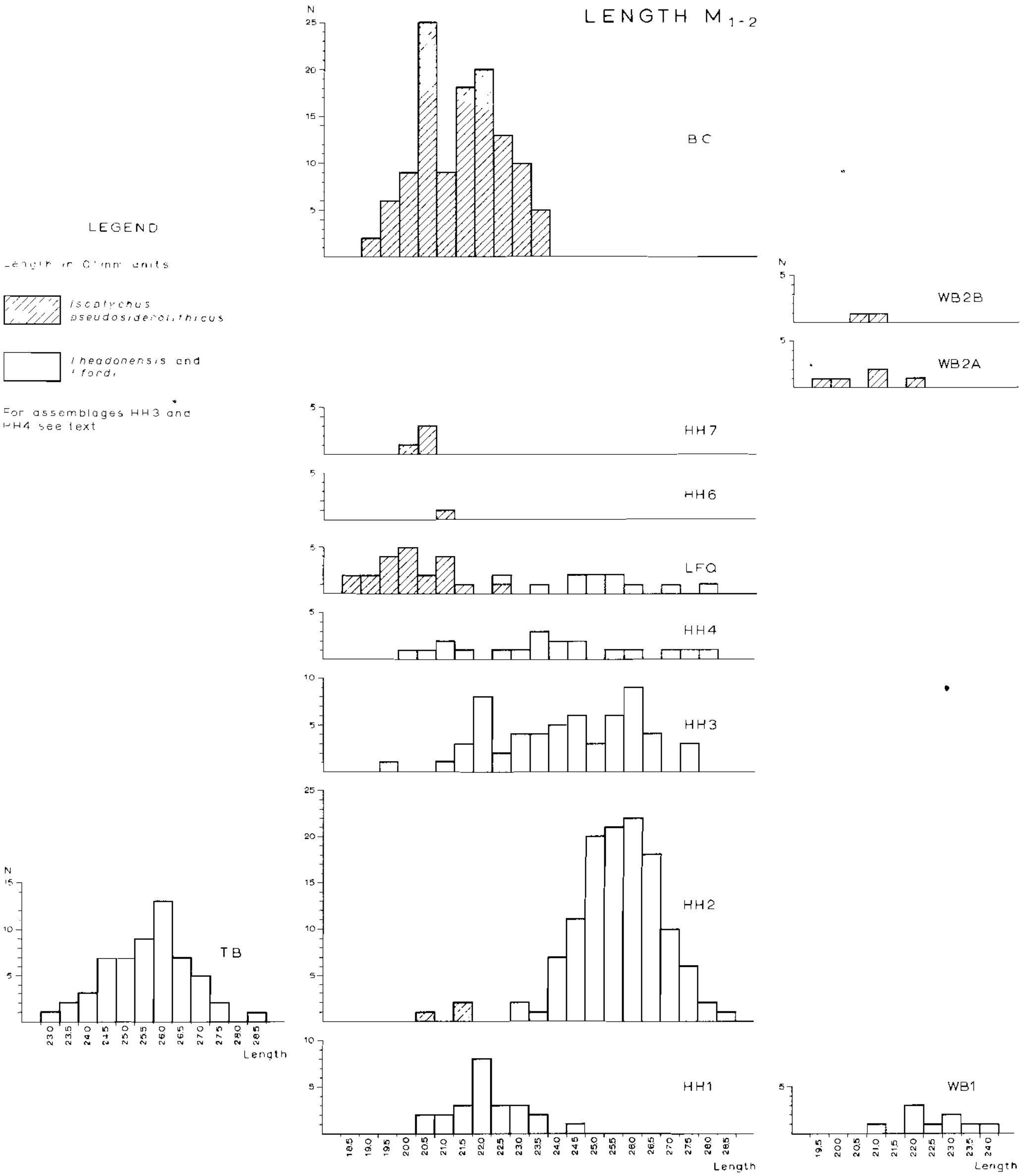
specimen	locality	formation	M_1	M_2	M_3
B.M.(N.H.) M14754	Yarmouth	Lower Hamstead Beds	simple	simple	–
F.C. BC(FD) 801	Bouldnor Cliff	id.	simple	simple	simple
F.C. WB2B(FD) 21	Whitecliff Bay 2B	Bembridge Marls	simple	simple	complex
F.C. WB2B(FD) 22	id.	id.	simple	simple	–
F.C. FI(FD) 1	Fishbourne	Osborne Beds	–	complex	complex
G.I.U. HH2 8–10	Headon Hill 2	Lower Headon Beds	simple	simple	simple
B.M.(N.H.) 30159a2	Hordle Cliff	id.	?	simple	simple
B.M.(N.H.) 30294	id. (?)	id. (?)	complex	complex	–
B.M.(N.H.) 36797	id.	id.	complex	simple	intermediate
B.M.(N.H.) 40212	id.	id.	?	complex	complex
S.M. C54124	id.	id.	complex	complex	complex
S.M. C54125	id.	id.	?	complex	complex
S.M. C54126	id.	id.	complex	simple	–
S.M. C54128	id.	id.	simple	simple	–
S.M. C30701	id.	id.	complex	complex	complex

The designation to a particular type of metalophid to some extent depends upon the stage of wear of the tooth. The type of metalophid could not be determined at advanced stages of wear. The frequencies of the types of metalophid have been recorded for the M_{1-2} only.

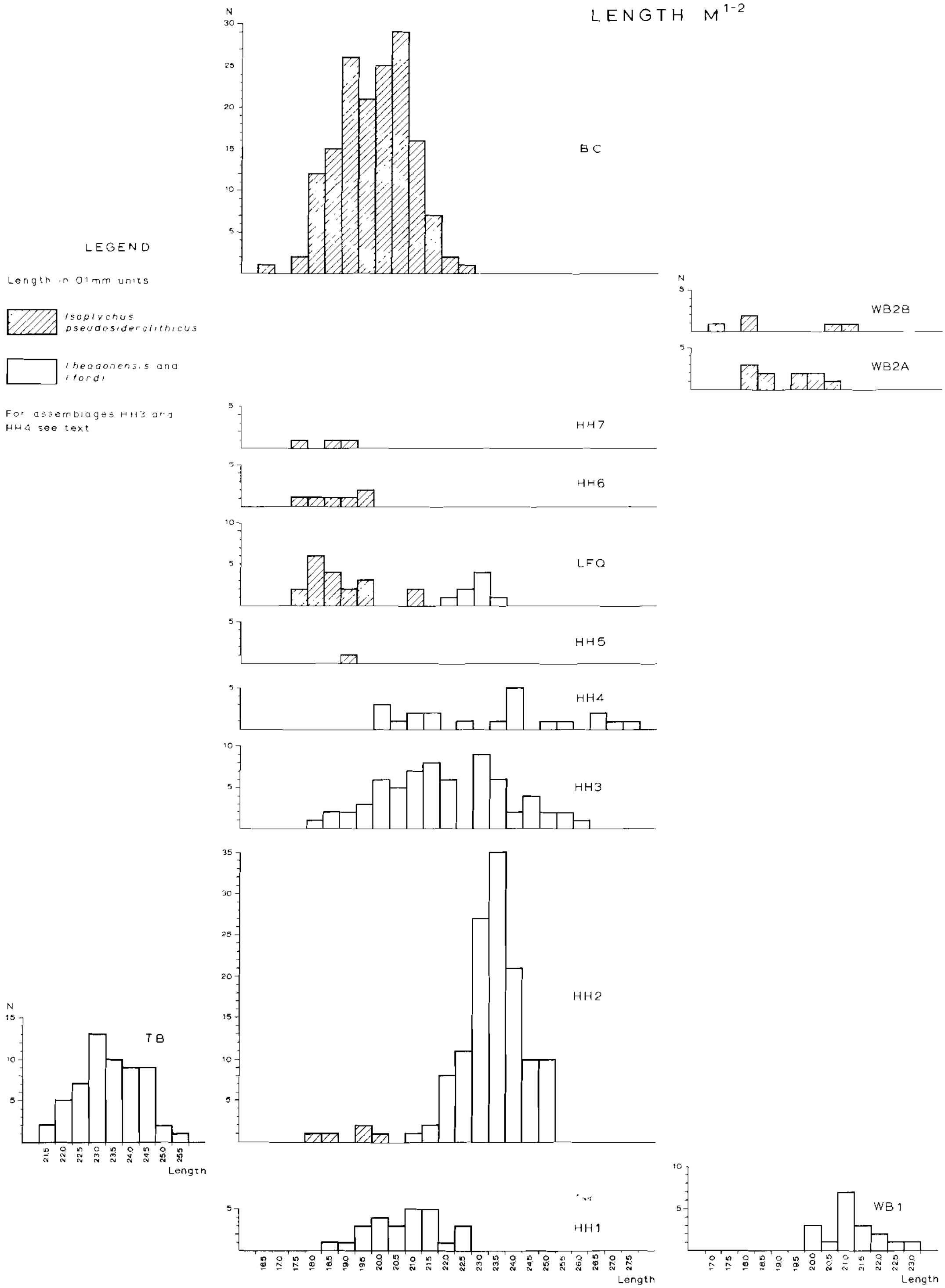
4.2.1.2. Results of measurements and counts on the assemblages from the Headon Hill – Bouldnor Cliff section.

Length of the M_{1-2} *and* M^{1-2}:

The distribution of the length of the teeth has been examined by means of histograms. Text-figs. 31 and 32 show histograms of the lengths of the M_{1-2} and M^{1-2} respectively. All histograms have been constructed with the same 0.5 (= 0.05 mm) intervals, in order to facilitate comparison. Cheek teeth from Headon Hill 2 and Bouldnor Cliff have only been taken into



Text-fig. 31 Histograms of the lengths of the M_{1-2} of *Isoptychus headonensis* n.sp., *Isoptychus fordi* Bosma and Insole, 1972 and *Isoptychus pseudosiderolithicus* De Bonis, 1964.



Text-fig. 32 Histograms of the lengths of the M^{1-2} of *Isoptychus headonensis* n.sp., *Isoptychus fordi* Bosma and Insole, 1972 and *Isoptychus pseudosiderolithicus* De Bonis, 1964.

account if both the length and the width could be measured.

Text-figs. 31 and 32 suggest that the samples from Headon Hill 1, Totland Bay, Headon Hill 6 and 7 and Bouldnor Cliff are single homogeneous groups. The samples from Headon Hill 2, 3 and 4, on the other hand, show a rather wide range of variation, while the frequency distributions seem to fit normal distributions less well.

From the appearance of the Headon Hill 2 histograms it might be concluded that both in the M_{1-2} and M^{1-2} two groups are present: a small group of short specimens and a large group of longer specimens. This view is supported by the similarity in frequency distribution of the length between the groups of long M_{1-2} and M^{1-2} from Headon Hill 2 and the M_{1-2} and M^{1-2} from Totland Bay. The latter locality has the same lithostratigraphic position as Headon Hill 2. The samples from Headon Hill 3 and 4 might also be mixtures of two groups, but their disentanglement is less clear.

Complexity of the dental pattern:

The numbers of small accessory cusps and crests in the M^{1-2} from Headon Hill 1 and 2, Totland Bay and Headon Hill 3 and 4 are very variable. In contrast with this, nearly all M^{1-2} from Headon Hill 5, 6 and 7 and Bouldnor Cliff show a simple dental pattern. The frequencies of the four degrees of complexity of the dental pattern in the M^{1-2} from Headon Hill 1 and 2 and Totland Bay are given in table X. The frequency distribution in the sample from Headon Hill 2 is based on 50 unworn or slightly worn specimens.

It has been indicated in the previous section (Length of the M_{1-2} and M^{1-2}) that the distribution of the length of the M_{1-2} and M^{1-2} from Headon Hill 2, 3 and 4 might suggest that the samples from these localities are mixtures of two groups. In the M^{1-2} from Headon Hill 2 the length of the tooth seems to interfere with the degree of complexity of the dental pattern, in such a way that all five short specimens show a simple dental pattern,

Locality	1	2	3	4	subtotal	undeterminable	total
Lacey's Farm Quarry	0	0	7	0	7	2	9
Totland Bay	0	3	37	11	51	9	60
Headon Hill 2	0	6	38	6	50	–	50
Whitecliff Bay 1	7	6	4	1	18	0	18
Headon Hill 1	9	10	5	2	26	2	28

Table X. Frequencies of the degrees of complexity of the dental pattern in the M^{1-2} of *Isoptychus headonensis* n.sp. and *Isoptychus fordi* Bosma and Insole, 1972 (1 = simple, 2 = slightly complex, 3 = moderately complex, 4 = very complex).

while the longer specimens have a slightly, moderately or very complex dental pattern. In table X and in calculating χ^2 and T′ (below) the group of short M^{1-2} with a simple pattern has been omitted.

The separation of the M^{1-2} from Headon Hill 3 and 4 into two groups is less obvious; therefore the frequency distributions of the degrees of complexity of the dental pattern in the M^{1-2} from Headon Hill 3 and 4 have neither been given in table X nor been compared with the frequency distributions in other samples.

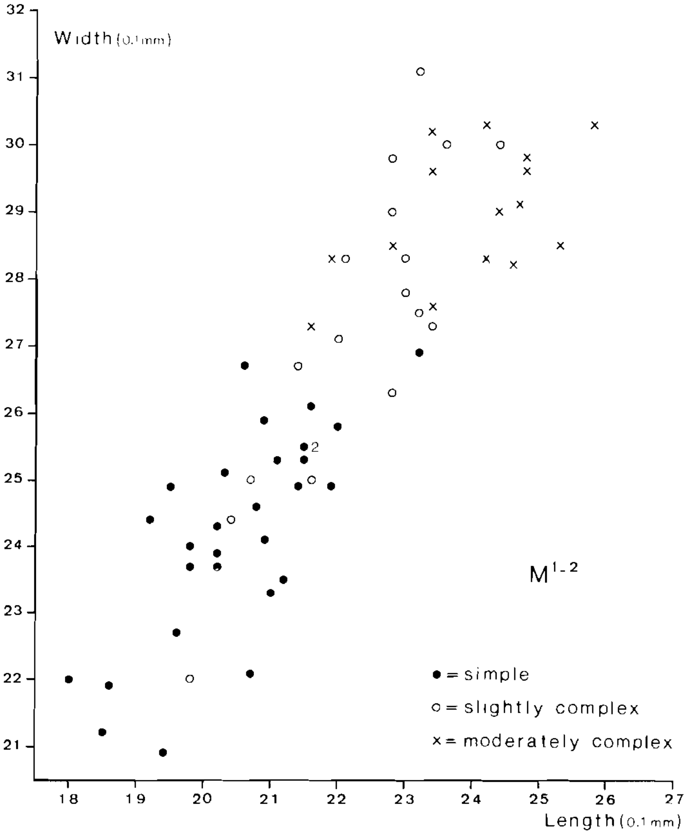
Whether the differences in frequency distribution between the samples from Headon Hill 1, Headon Hill 2 and Totland Bay are significant has been tested with the χ^2 test (for independence). The values of χ^2 show that the samples from Headon Hill 2 and Totland Bay might have been taken from the same population ($\chi^2 = 2.47$, with 2 degrees of freedom). There appear to be significant differences in frequency distribution between the M^{1-2} from Headon Hill 1 and 2 ($\chi^2 = 33.02$, with 3 degrees of freedom) and between the M^{1-2} from Headon Hill 1 and Totland Bay ($\chi^2 = 39.39$, with 3 degrees of freedom). The number of specimens with a moderately or very complex dental pattern increases in upward stratigraphic direction.

Whether the length of the M^{1-2} is equally distributed in each category of complexity of the dental pattern has been tested with the rank-sum statistic T′. The values of T′ are given in table XI. These values show that there are significant differences in length between the specimens with a slightly and a moderately or very complex dental pattern in the M^{1-2} from Headon Hill 2 and Totland Bay. The M^{1-2} with a slightly complex pattern are shorter than those with a moderately or very complex pattern.

Locality	1 versus 2	1 versus 3	1 versus 4	2 versus 3	2 versus 4	3 versus 4
Headon Hill 4	*68*(8,6)	*30*(8,3)	*42*(8,4)	22.5(6,3)	*34*(6,4)	8(3,4)
Headon Hill 3	*655*(31,18)	*671.5*(31,17)	–	*400.5*(18,17)	–	–
Totland Bay	–	–	–	*22*(3,36)	*6*(3,11)	300.5(36,11)
Headon Hill 2	–	–	–	*33.5*(6,38)	*23*(6,6)	131.5(38,6)
Whitecliff Bay 1	41.5(7,6)	*38*(7,4)	8(7,1)	*32*(6,4)	7(6,1)	5(4,1)
Headon Hill 1	90.5(9,9)	38(9,4)	15.5(9,2)	36(9,4)	16(9,2)	6(4,2)

Table XI. T′ values for comparison of the distribution of the length in the categories of complexity of the dental pattern in the M^{1-2} of *Isoptychus headonensis* n.sp., *Isoptychus fordi* Bosma and Insole, 1972 and *Isoptychus pseudosiderolithicus* De Bonis, 1964 (1 = simple, 2 = slightly complex, 3 = moderately complex, 4 = very complex; sample sizes in parentheses; significant values of T′ in italics).

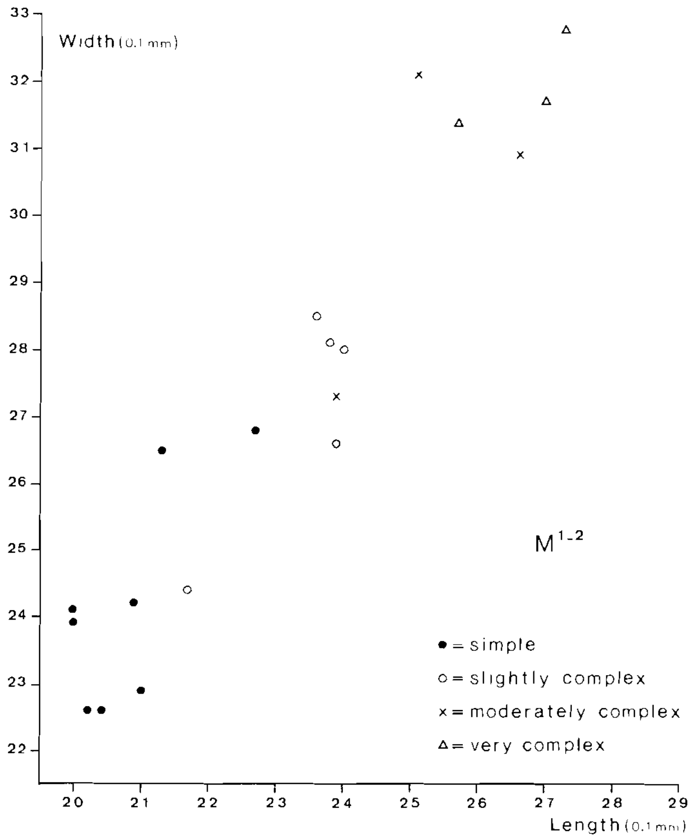
The same test has been applied to the M^{1-2} from Headon Hill 3 and 4. The dental pattern of the M^{1-2} from Headon Hill 3 is simple, slightly complex or moderately complex; the M^{1-2} from Headon Hill 4 show all four degrees of complexity. The relation between the size of the tooth and the degree of complexity of the dental pattern is shown graphically in text-figs. 33 and 34. The values of T', given in table XI, prove that there are significant differences in length between the specimens in each category of complexity in the M^{1-2} from Headon Hill 3. The M^{1-2} with a simple pattern are shorter than those with a slightly or moderately complex pattern, while the M^{1-2} with a slightly complex pattern are shorter than those with a moderately complex pattern. In the M^{1-2} from Headon Hill 4 there are significant differences in length between the specimens with a simple dental



Text-fig. 33 Distribution of the degrees of complexity of the dental pattern relative to the size of the teeth in the M^{1-2} of *Isoptychus pseudosiderolithicus* De Bonis, 1964 and *Isoptychus fordi* Bosma and Insole, 1972 from Headon Hill 3.

pattern and those with a slightly, moderately or very complex dental pattern; there are also significant differences in length between the specimens with a slightly and those with a very complex dental pattern. The M^{1-2} with a simple pattern are shorter than those with a more complex pattern, while the M^{1-2} with a slightly complex pattern are shorter than those with a very complex pattern.

It is notable, that there are no significant differences in length of the M^{1-2} in each category of complexity in the sample from Headon Hill 1. None of the samples shows a significant difference in length between the M^{1-2} with a moderately complex dental pattern and those with a very complex dental pattern.



Text-fig. 34 Distribution of the degrees of complexity of the dental pattern relative to the size of the teeth in the M^{1-2} of *Isoptychus pseudosiderolithicus* De Bonis, 1964 and *Isoptychus fordi* Bosma and Insole, 1972 from Headon Hill 4.

Structure of the metalophid:

The M_{1-2} from Headon Hill 1 and 2, Totland Bay and Headon Hill 3 and 4 show a simple metalophid, a metalophid of intermediate type or a complex metalophid, whereas all M_{1-2} from Headon Hill 6 and 7 and Bouldnor Cliff show a simple metalophid. The frequencies of the three types of metalophid in the M_{1-2} from Headon Hill 1 and 2 and Totland Bay are given in table XII.

Locality	1	2	3	subtotal	undeter-minable	total
Lacey's Farm Quarry	0	0	11	11	2	13
Totland Bay	2	2	40	44	14	58
Headon Hill 2	6	3	63	72	49	121
Whitecliff Bay 1	1	0	4	5	4	9
Headon Hill 1	6	4	6	16	11	27

Table XII. Frequencies of the types of metalophid in the M_{1-2} of *Isoptychus headonensis* n.sp. and *Isoptychus fordi* Bosma and Insole, 1972 (1 = simple, 2 = intermediate, 3 = complex).

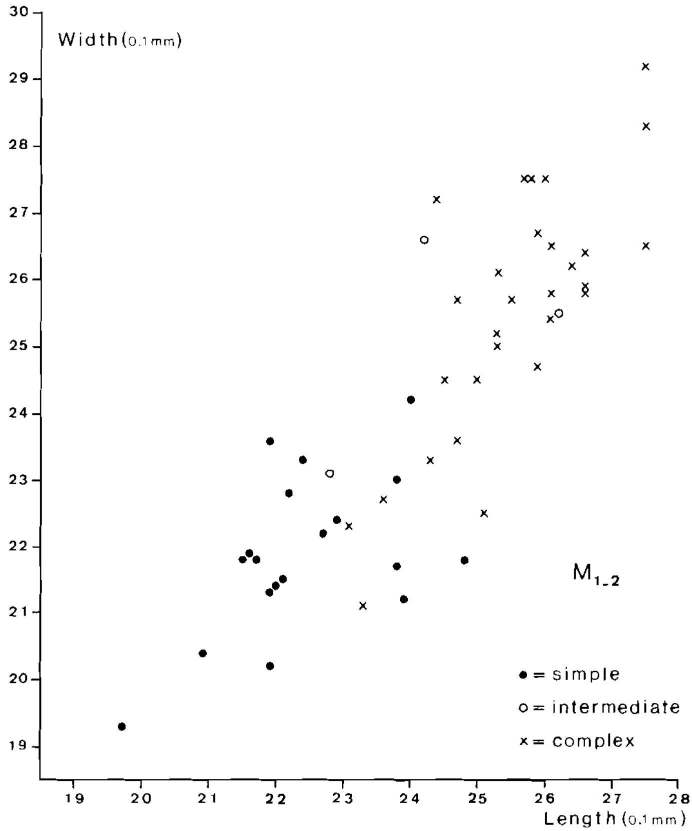
The supposition that two groups are present in the M_{1-2} (and M^{1-2}) from Headon Hill 2, 3 and 4 (see preceding sections) is supported by the fact that the three very short M_{1-2} from Headon Hill 2 all have a simple metalophid. The other M_{1-2} from Headon Hill 2 show a simple metalophid, a metalophid of intermediate type or a complex metalophid. In table XII and in calculating T′ (below) the three short specimens have been omitted. Table XII neither includes the frequencies of the types of metalophid in the samples from Headon Hill 3 and 4, because of the presumably mixed nature of these samples. For the same reason, the frequencies of the types of metalophid in the samples from Headon Hill 3 and 4 have not been compared with the frequencies in other samples.

In the M_{1-2} from Headon Hill 1 the frequencies of the three types of metalophid are about equal, whereas in the M_{1-2} from Headon Hill 2 and Totland Bay the majority of the specimens shows a complex metalophid. The differences in frequency distribution between the samples from Headon Hill 1, Headon Hill 2 and Totland Bay could not be tested statistically, as the observed frequencies are too small for χ^2 approximation.

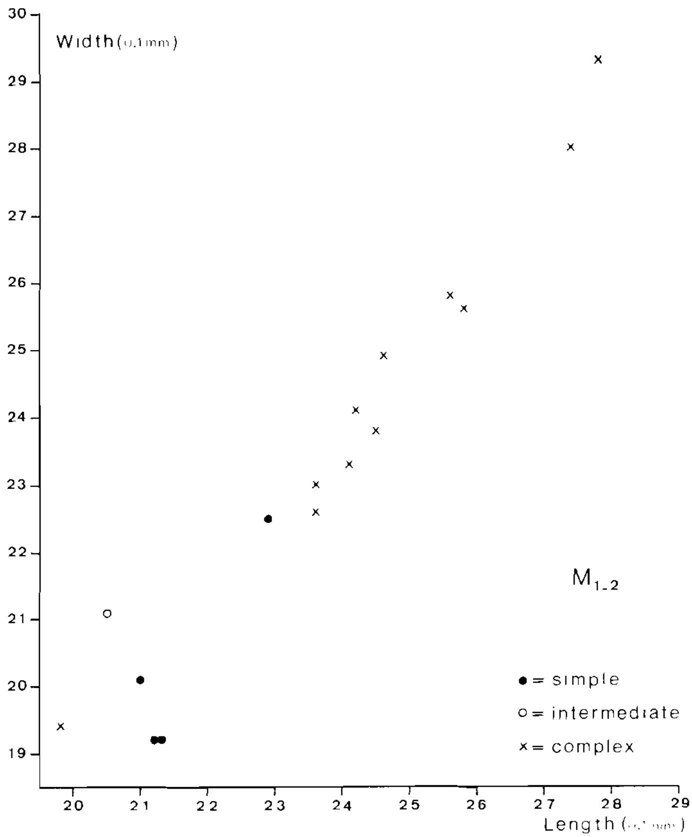
Whether the length of the M_{1-2} from Headon Hill 1 and 2 and Totland Bay is equally distributed in each category of structure of the metalophid has been tested with the rank-sum test. The values of T′ are given in table XIII. It appears that there is a significant difference in length between the

Locality	1 versus 2	1 versus 3	2 versus 3
Headon Hill 4	1(4,1)	*14*(4,11)	2(1,11)
Headon Hill 3	*61*(21,3)	*264.5*(21,31)	35(3,31)
Totland Bay	3.5(2,2)	48(2,40)	54(2,40)
Headon Hill 2	9.5(6,3)	299.5(6,63)	93.5(3,63)
Whitecliff Bay 1	–	2(1,4)	–
Headon Hill 1	20.5(6,4)	29(6,6)	*12*(4,6)

Table XIII. T' values for comparison of the distribution of the length in the categories of structure of the metalophid in the M_{1-2} of *Isoptychus headonensis* n.sp., *Isoptychus fordi* Bosma and Insole, 1972 and *Isoptychus pseudosiderolithicus* De Bonis, 1964 (1 = simple, 2 = intermediate, 3 = complex; sample sizes in parentheses; significant values of T' in italics).



Text-fig. 35 Distribution of the three types of metalophid relative to the size of the teeth in the M_{1-2} of *Isoptychus pseudosiderolithicus* De Bonis, 1964 and *Isoptychus fordi* Bosma and Insole, 1972 from Headon Hill 3.



Text-fig. 36 Distribution of the three types of metalophid relative to the size of the teeth in the M_{1-2} of *Isoptychus pseudosiderolithicus* De Bonis, 1964 and *Isoptychus fordi* Bosma and Insole, 1972 from Headon Hill 4.

specimens with a metalophid of intermediate type and those with a complex metalophid in the M_{1-2} from Headon Hill 1. The M_{1-2} with a metalophid of intermediate type are shorter than those with a complex metalophid.

The relation between the size of the tooth and the structure of the metalophid in the M_{1-2} from Headon Hill 3 and 4 is represented graphically in text-figs. 35 and 36. Application of the rank-sum test (see for values of T′ table XIII) to the sample from Headon Hill 3 reveals significant differences in length between the specimens with a simple metalophid and those with a metalophid of intermediate type or a complex metalophid. The M_{1-2} with a simple metalophid are shorter than those with another type of metalophid. In the sample from Headon Hill 4 there is a significant difference in length between the specimens with a simple metalophid and those with a complex metalophid. The former are shorter than the latter.

4.2.1.3. Results of measurements and counts on the assemblages from the Whitecliff Bay section.

Length of the M_{1-2} *and* M^{1-2}*:*

Histograms of the lengths of the M_{1-2} and M^{1-2} from Whitecliff Bay 1, 2A and 2B are given in text-figs. 31 and 32. These histograms suggest that the samples from Whitecliff Bay 1, 2A and 2B are single homogeneous groups.

Whitecliff Bay 1 is lithostratigraphically correlated with the Lower Headon Beds. Text-figs. 31 and 32 demonstrate that the lengths of the M_{1-2} and M^{1-2} from Whitecliff Bay 1 are very similar to the lengths of the M_{1-2} and M^{1-2} from Headon Hill 1. This similarity is borne out by the low values of t, calculated in order to test the differences in length between the M_{1-2} and M^{1-2} from the two localities statistically ($t = 0.902$, with 31 degrees of freedom ($P > 0.05$) and $t = 1.743$, with 42 degrees of freedom ($P > 0.05$), respectively).

Whitecliff Bay 2A and 2B are situated in the Bembridge Marls. Their faunas may be somewhat younger than those from Headon Hill 6 and 7, as these localities are tentatively correlated with the Bembridge Limestone on lithological grounds. The faunas of Whitecliff Bay 2A and 2B are considered to be older than the fauna of Bouldnor Cliff. Text-figs. 31 and 32 show that the lengths of the M_{1-2} and M^{1-2} from Whitecliff Bay 2A and 2B fall within the ranges of the length of the M_{1-2} and M^{1-2} from Bouldnor Cliff.

Complexity of the dental pattern:

The M^{1-2} from Whitecliff Bay 1 show four degrees of complexity, whereas the M^{1-2} from Whitecliff Bay 2A and 2B all have a simple dental pattern. The frequencies of the degrees of complexity of the dental pattern in the M^{1-2} from Whitecliff Bay 1 are given in table X. This table shows the similarity in frequency distribution between the samples from Whitecliff Bay 1 and Headon Hill 1. Application of the χ^2 test confirms that these samples might have come from the same population ($\chi^2 = 0.17$, with 2 degrees of freedom).

Values of T', given in table XI, reveal significant differences in length between the M^{1-2} from Whitecliff Bay 1 with a simple or slightly complex dental pattern and those with a moderately complex dental pattern. The latter are longer.

Structure of the metalophid:

One out of the five M_{1-2} from Whitecliff Bay 1 shows a simple metalophid, while the other four specimens show a complex metalophid (see also table XII). Application of the rank-sum test does not reveal a significant difference in length between the specimen with a simple metalophid and the specimens with a complex metalophid (see for value of T' table XIII). The small number of observations does not allow comparison of the frequency distribution of the types of metalophid in the M_{1-2} from Whitecliff Bay 1 with that in other samples by means of the χ^2 test.

The M_{1-2} from Whitecliff Bay 2A and 2B all have a simple metalophid.

4.2.1.4. Results of measurements and counts on the assemblages from Lacey's Farm Quarry.

Bosma and Insole (1972) described two species of *Isoptychus* from the Osborne Beds. These species, which they called *I. aquatilis* (Gervais, 1848–1852) and *I. fordi* n. sp., occur together in two localities, where they can be clearly distinguished by differences in dental pattern and teeth dimensions. The determination of one of the species as *I. aquatilis* is incorrect; this species has to be classified as *I. pseudosiderolithicus* De Bonis, 1964, because of the small size of its cheek teeth (see section 4.2.2.1.3). In this paper discussions are limited to *I. pseudosiderolithicus* and *I. fordi* from Lacey's Farm Quarry (University of Bristol site no. 6911).

Length of the M_{1-2} and M^{1-2}:

Histograms of the lengths of the M_{1-2} and M^{1-2} are given in text-figs. 31 and 32. The wide ranges and the bimodality of the histograms reflect the differences in size between *I. pseudosiderolithicus* and *I. fordi. I. fordi* is larger than *I. pseudosiderolithicus.*

Complexity of the dental pattern:

All M^{1-2} of *I. pseudosiderolithicus* have a simple dental pattern, whereas all M^{1-2} of *I. fordi* have a moderately complex dental pattern. Table X includes the M^{1-2} of *I. fordi.* The predominance of M^{1-2} with a moderately complex pattern is also found in the M^{1-2} from Headon Hill 2 and Totland Bay.

Structure of the metalophid:

All M_{1-2} of *I. pseudosiderolithicus* have a simple metalophid; all M_{1-2} of *I. fordi* have a complex metalophid. Table XII includes the M_{1-2} of *I. fordi.* M_{1-2} with a complex metalophid also preponderate over M_{1-2} with a simple metalophid or a metalophid of intermediate type in the assemblages from Headon Hill 2 and Totland Bay.

4.2.1.5. **Discussion.**

The M_{1-2} from Headon Hill 1 with a metalophid of intermediate type are significantly shorter than those with a complex metalophid; the M^{1-2} from Totland Bay with a slightly complex dental pattern are significantly shorter than those with a moderately or very complex dental pattern, while the M^{1-2} from Whitecliff Bay 1 with a simple or slightly complex dental pattern are significantly shorter than those with a moderately complex dental pattern. Apparently, there is some correlation between the length of the tooth and the structure of the metalophid in the M_{1-2} and between the length of the tooth and the degree of complexity of the dental pattern in the M^{1-2}. It is emphasized that the M_{1-2} and M^{1-2} from Headon Hill 1, Totland Bay and Whitecliff Bay 1 are single homogeneous groups with regard to their lengths.

The correlation between the length of the tooth and the type of dental structure may be the only cause of the frequently significant differences in length between the M_{1-2} in the three categories of structure of the metalophid and between the M^{1-2} in the categories of complexity of the dental pattern in the assemblages from Headon Hill 3 and 4; the separation of the M_{1-2} from Headon Hill 2 into a group of short specimens with a simple metalophid and a group of longer specimens with a simple metalophid, a metalophid of intermediate structure or a complex metalophid; the separation of the M^{1-2} from Headon Hill 2 into a group of short specimens with a simple dental pattern and a group of longer specimens with a slightly, moderately or very complex dental pattern; the separation of the M_{1-2} from Lacey's Farm Quarry into a group of short specimens with a simple metalophid and a group of longer specimens with a complex metalophid; the separation of the M^{1-2} from Lacey's Farm Quarry into a group of short specimens with a simple dental pattern and a group of longer specimens with a moderately complex dental pattern.

However, these facts may better be interpreted as being caused by the presence of two species of *Isoptychus* in the faunas from Headon Hill 2, 3 and 4 and Lacey's Farm Quarry: a species with relatively small cheek teeth and a simple dental structure, and a species with relatively large cheek teeth and a more complex dental structure.

This view is supported by the wide ranges and irregular distributions of the length in the M_{1-2} and M^{1-2} from Headon Hill 2, 3 and 4 and Lacey's Farm Quarry and by the observations that the M_{1-2} and M^{1-2} from Headon Hill 6 and 7, Whitecliff Bay 2A and 2B and Bouldnor Cliff are relatively short, while all M_{1-2} show a simple metalophid and nearly all M^{1-2} show a simple dental pattern.

4.2.1.6. Conclusions.

In the Paleogene succession of the Isle of Wight two lineages of the genus *Isoptychus* are present. Members of these lineages occur together in the faunas from Headon Hill 2, 3 and 4 and Lacey's Farm Quarry, showing differences in the dimensions of the teeth, the degree of complexity of the dental pattern and the structure of the metalophid. The assemblages of relatively small cheek teeth with a simple dental pattern and a simple metalophid are considered to belong to *I. pseudosiderolithicus* De Bonis, 1964. The assemblages of relatively large cheek teeth with a more complex dental pattern and a more complex metalophid are referred to as *I. fordi* Bosma and Insole, 1972. The individual teeth of *Isoptychus* from Headon Hill 2 and Lacey's Farm Quarry may be distributed between the two species without much doubt. Whether a particular tooth from Headon Hill 3 or 4 belongs to one species or the other can only be decided when it takes an extreme position in the variation.

In Totland Bay *Isoptychus* is only represented by *I. fordi.* There are no differences in length and dental structure between the M_{1-2} and M^{1-2} of *I. fordi* from Headon Hill 2 and Totland Bay.

In the youngest faunas, those from Headon Hill 5, 6 and 7, Whitecliff Bay 2A and 2B and Bouldnor Cliff, *Isoptychus* is only represented by *I. pseudosiderolithicus.*

There are slight differences in the dimensions of the teeth between the assemblages from successive stratigraphic levels, both in *I. fordi* and *I. pseudosiderolithicus.* These differences are not considered important enough to be expressed in the formal taxonomy.

In the oldest faunas, those from Headon Hill 1 and Whitecliff Bay 1, one species is present, which has cheek teeth that are intermediate in size between those of *I. pseudosiderolithicus* and *I. fordi* (see text-figs. 31 and 32). There are significant differences in frequency distribution of the four degrees of complexity of the dental pattern between the M^{1-2} from Headon Hill 1 and Whitecliff Bay 1 on the one side and the M^{1-2} of *I. fordi* from Headon Hill 2 and Totland Bay on the other. The dental pattern in the M^{1-2} from Headon Hill 1 and Whitecliff Bay 1 is less complex than that in the M^{1-2} of *I. fordi* from Headon Hill 2 and Totland Bay, although it is more complex than that in the M^{1-2} of *I. pseudosiderolithicus.* There are also significant differences in frequency distribution of the three types of metalophid between the M_{1-2} from Headon Hill 1 and Whitecliff Bay 1 on the one side and the M_{1-2} of *I. fordi* from Headon Hill 2 and Totland Bay on the other. The metalophid is less complex in the M_{1-2} from Headon Hill 1 and

Whitecliff Bay 1 than in the M_{1-2} of *I. fordi* from Headon Hill 2 and Totland Bay, but more complex than in the M_{1-2} of *I. pseudosiderolithicus*. There are no differences in length and dental structure between the M_{1-2} and M^{1-2} from Headon Hill 1 and Whitecliff Bay 1. The species from Headon Hill 1 and Whitecliff Bay 1 will be described as a new species, *I. headonensis*. *I. headonensis* is considered to be the ancestor of *I. fordi*. It is supposed, that *I. fordi* developed from *I. headonensis* by selection in favour of large and complex cheek teeth.

The ancestry of *I. pseudosiderolithicus* remains uncertain. In a currently held view (Hartenberger, 1973) *I. pseudosiderolithicus* is considered to be evolved from *I. euzetensis* (Depéret, 1917), a species known from Euzet, Fons 2 and 4, Perrière, Malpérié (France) and Sosis (Spain).

4.2.2. Subfamily THERIDOMYINAE Alston, 1876

4.2.2.1. Genus Isoptychus Pomel, 1853

Original reference: Pomel (1853), p.34-36.
Type-species: *Theridomys aquatilis* Gervais, 1848-1852.

Emended diagnosis:

Theridomyinae with slightly hypsodont cheek teeth. The dental pattern is characterized by the presence of three main synclines or synclinids which show little difference in length. The upper cheek teeth are always provided with a syncline IV, which is short and shallow. In the lower cheek teeth the sinusid is shorter than the synclinids II, III and IV; in the upper cheek teeth the sinus is shorter than the synclines I, II and III. The original cusps are clearly distinguishable. In the lower molars the metalophid is one single crest, or it is double, consisting of an anterior and a posterior branch; the posterior branch is either complete or incomplete.

The incisive foramen extends at least to close to the premolar. The anterior limit of the internal nares is usually situated behind the anterior border of the M^3, sometimes in line with that border, but never anterior to it. The teeth rows are parallel. The palate is rather wide.

Remark:

Thus defined there is no need to recognize two (sub)genera, *Isoptychus* and *Trechomys*. *Trechomys* is considered to be a synonym of *Isoptychus* (cf. Vianey-Liaud, 1972c).

Differential diagnosis:

Isoptychus differs from *Theridomys* in its less hypsodont cheek teeth, in the nearly equal length of the synclinids II, III and IV and of the synclines I, II and III, and in the shorter sinusid and sinus.

Isoptychus differs from *Pseudoltinomys* in the larger size of the premolars relative to the molars, in the triangular-shaped cross-section of the incisors, in the absence of an antesinusid in most lower cheek teeth and in the not-confluent sinus and syncline II of most upper cheek teeth.

Discussion:

Vianey-Liaud (1972b) and Hartenberger (1973) considered *Isoptychus* to be synonymous with *Theridomys,* as they believed that *Theridomys* species evolved from *Isoptychus* species. In our opinion, supposed phylogenetical relations are no good reason for the allocation to one genus. Most species of *Isoptychus* and *Theridomys* show consistent differences in dental structure and therefore it is preferred to maintain both genera. Species proving to be intermediate in dental structure between *Isoptychus* and *Theridomys* may be referred to one genus or the other in an arbitrary way.

Since *Isoptychus* was defined, numerous species have been referred to this genus. Occasional species have been referred to *Trechomys* or *Theridomys* instead of to *Isoptychus,* in consequence of the ambiguity about the definitions of the three genera. Some species originally described as *Isoptychus* species have afterwards been transferred to other genera: *Pseudoltinomys cuvieri* (Pomel, 1853), *Pseudoltinomys intermedius* (Schlosser, 1884), *Pseudoltinomys pusillus* (Schlosser, 1884) and *Oltinomys platyceps* (Filhol, 1876). Other species have been shown to be nomina nuda: *Isoptychus auberyi* Pomel, 1853 (De Bonis, 1964), *Isoptychus antiquus* Pomel, 1853, (De Bonis, 1964), *Theridomys siderolithicus* Pictet, 1856 (Hartenberger, 1973) and *Theridomys gaudini* Pictet and Humbert, 1869 (Hartenberger, 1973).

The genus *Isoptychus* is considered by us to comprise the following species: *I. euzetensis* (Depéret, 1917), *I. pseudosiderolithicus* De Bonis, 1964, *I. golpei* (Hartenberger, 1973), *I. aquatilis* (Gervais, 1848-1852), *I. bonduelli* (Lartet, 1869), *I. fordi* Bosma and Insole, 1972 and *I. headonensis* n. sp.

The question whether *Isoptychus vassoni* Pomel, 1853, *Theridomys rotundidens* Schlosser, 1884 and *Theridomys parvulus* Schlosser, 1884 belong to *Isoptychus* or to *Theridomys* is not discussed, as we have not been able to study the type-specimens.

4.2.2.1.1. **Isoptychus headonensis** n. sp. (Plate I, figs. 1–11; plate II, figs. 1–4)

Diagnosis:

A species of *Isoptychus* with cheek teeth frequently provided with accessory cuspules and crests. Metalophid in the lower molars single or double, in the latter case consisting of an anterior and a posterior branch; the posterior branch may be complete or incomplete.

Differential diagnosis:

I. headonensis differs from *I. fordi* in its smaller cheek teeth, in the less frequent occurrence of accessory cuspules and crests and in the less frequent occurrence of a double metalophid.

Derivatio nominis: After the name of the type-locality, Headon Hill.

Holotype: An isolated M_{1-2} (G.I.U. HH1 22) (Plate I, fig. 3).

Measurements holotype: 21.7 x 20.4. Measurements of the type-series are given in table XIV.

Paratypes: 9 D_4 (HH1 1–9); 4 P_4 (HH1 11–14); 26 M_{1-2} (HH1 21, 23–47); 8 M_3 (HH1 51–58); 11 D^4 (HH1 61–70, 80); 5 P^4 (HH1 71–75); 28 M^{1-2} (HH1 81–108); 6 M^3 (HH1 111–116).

Type-locality: Headon Hill 1 (Isle of Wight, England).

Formation: Lower Headon Beds.

Stratigraphic range: Lower part Lower Headon Beds.

	Length				Width		
	N	range	$\bar{X}$	s	N	range	$\bar{X}$
D_4	3	25.4–28.2	26.87	1.40	8	15.1–17.4	16.43
P_4	4	24.6–26.8	25.50	0.93	4	19.3–22.7	21.00
M_{1-2}	24	20.3–24.7	22.17	0.99	23	19.8–25.1	22.11
M_3	8	22.0–24.4	23.26	0.96	8	18.9–22.4	20.21
D^4	10	20.3–24.3	22.57	1.24	10	19.0–21.5	19.97
P^4	3	19.6–22.8	21.47	1.67	5	21.9–25.1	23.50
M^{1-2}	26	18.6–22.4	20.75	1.03	22	21.3–27.5	24.46
M^3	6	18.1–21.3	19.57	1.45	5	18.7–23.0	20.70

Table XIV. Measurements of the cheek teeth of *Isoptychus headonensis* n.sp. from the type-locality Headon Hill 1. (N = number of observations, $\bar{X}$ = mean value, s = standard deviation of the sample).

Further material:
Whitecliff Bay 1: 3 D_4, 9 M_{1-2}, 3 M_3, 11 D^4, 3 P^4, 18 M^{1-2}, 1 M^3.
Fragment of upper jaw with M^1 and M^2.

Measurements of the isolated cheek teeth from Whitecliff Bay 1 are given in table XV.

Measurements of the cheek teeth in the jaw fragment: M^1: 23.3 x –; M^2: 22.5 x 29.9.

	Length				Width		
	N	range	$\bar{X}$	s	N	range	$\bar{X}$
D_4	2	25.5–29.3	27.40	2.69	2	15.2–17.9	16.55
M_{1-2}	9	21.0–24.1	22.52	0.99	9	20.8–25.0	22.49
M_3	2	22.9–26.0	24.45	2.19	3	19.2–23.0	20.67
D^4	8	21.7–24.3	23.11	0.89	11	19.5–20.9	20.04
P^4	3	21.4–24.8	22.83	1.76	3	23.1–27.0	25.37
M^{1-2}	18	20.0–23.1	21.26	0.83	13	22.4–27.6	24.96
M^3	1	–	20.4	–	1	–	23.0

Table XV. Measurements of the isolated cheek teeth of *Isoptychus headonensis* n.sp. from Whitecliff Bay 1. (N = number of observations, $\bar{X}$ = mean value, s = standard deviation of the sample).

Description:

D_4: The deciduous teeth are less hypsodont than the permanent ones. Their pattern is characterized by a large number of accessory cuspules and crests. Yet the main cusps and crests can be clearly distinguished. Most specimens show a cuspule or short transverse crest in the deeper portion of the sinusid.

P_4: The structure of the metalophid in the premolars resembles the variable structure of the metalophid in the molars. The specimen figured on plate I, fig. 2 differs from the other P_4 in that synclinid III is closed lingually by a crest nearly as high as the mesolophid.

M_{1-2}, M_3: The molars show a simple metalophid, a metalophid of intermediate type or a complex metalophid (see section 4.2.1.1.). Frequencies of the three types of metalophid in the M_{1-2} are given in table XII. Among 6 slightly worn M_3 from Headon Hill 1, 3 specimens show a simple metalophid, 1 specimen shows a metalophid of intermediate type and 2 specimens show a complex metalophid. The M_3 from Whitecliff Bay 1 both show a simple metalophid. The mesolophid is interrupted in the middle in one specimen (Plate I, fig. 7), while it is narrow at its lingual side in another. The width of synclinid III is variable. In two M_{1-2} a small cusp is present at the bottom of the sinusid; in another a sharp vertical ridge extends from this bottom up to about half the height of the tooth.

D^4: The milk teeth are less hypsodont than the (pre)molars. The occlusal surface shows a large number of accessory cuspules and crests. Yet the main cusps can be clearly distinguished. In one specimen the lingual connection between the metaloph and the posteroloph is interrupted. In occasional specimens the endoloph is interrupted. Frequently a cuspule of variable size is situated at the bottom of the sinus.

P^4, M^{1-2}, M^3: The P^4, M^{1-2} and M^3 show a simple, slightly complex, moderately complex or very complex dental pattern (see section 4.2.1.1). Frequencies of the degrees of complexity in the M^{1-2} are given in table X. Among 4 unworn and slightly worn P^4 from Headon Hill 1, 2 specimens show a moderately complex dental pattern and 2 specimens a very complex dental pattern. The single slightly worn P^4 from Whitecliff Bay 1 shows a very complex dental pattern. Apparently the dental pattern is more complex in the P^4 than it is in the M^{1-2}. Among 4 unworn and slightly worn M^3 from Headon Hill 1, 1 specimen shows a simple dental pattern, 1 specimen a slightly complex dental pattern, while 2 specimens show a moderately complex dental pattern. The pattern of the single M^3 from Whitecliff Bay 1 is moderately complex. In one P^4 the mesoloph is interrupted in the middle. In two M^{1-2} and one M^3 the lingual connection between the metaloph and the posteroloph is interrupted. Usually syncline IV in the M^3 is well developed. In one M^3 the buccal part of the posteroloph is absent, which causes syncline IV to be present as a shallow depression only. In the specimen figured on plate I, fig. 9 and in one M^{1-2} the endoloph is interrupted. In a few specimens syncline II is closed buccally by a crest as high as the main crests.

Remarks:

The material of *Isoptychus* from the Lower Headon Beds at Hordle Cliff (Hampshire, England) stored in the British Museum (Natural History) and the Sedgwick Museum (Cambridge) also belongs to *I. headonensis*.

Fragments of upper jaws of *I. headonensis* from Hordle Cliff show that there is some difference in position of the posterior border of the incisive foramen between this species and *I. pseudosiderolithicus*. In the specimens of *I. headonensis* (B.M.(N.H.) 25228, 30159a6 (Plate II, fig. 4) and M12567, S.M. C54133 and C54136) the posterior border of the incisive foramen is situated in line with the anterior border of the P^4 or slightly anterior to this border. Four fragments of upper jaws of *I. pseudosiderolithicus* from Whitecliff Bay 2B and Bouldnor Cliff, on the other hand, have the posterior border of the incisive foramen in line with the posterior half of the P^4 (Plate II, fig. 5). The difference in position of the posterior border of the incisive foramen supports our conclusion that *I. headonensis* and *I. pseudosiderolithicus* belong to different lineages (see section 4.2.1.6). Unfortunately, there are no data available on the palatal structure in *I. fordi* to check the lineage-constant character of the position of the incisive foramen.

4.2.2.1.2. **Isoptychus fordi Bosma and Insole, 1972**

Original reference: Bosma and Insole (1972), p. 140–143; plate I, figs. 3, 5, 7, 9 and 10.

Differential diagnosis:

I. fordi differs from *I. headonensis* in its larger cheek teeth, in the more frequent occurrence of accessory cuspules and crests and in the more frequent occurrence of a double metalophid.

I. fordi differs from *I. bonduelli* in showing a dental pattern with many accessory cuspules and crests and a frequently completely double metalophid.

Holotype: An isolated M_{1-2} (B.M.(N.H.) M29431).

Type-locality: Lacey's Farm Quarry (University of Bristol site no. 6911), Isle of Wight, England.

Stratigraphic range on the Isle of Wight: Upper part Lower Headon Beds, Upper Headon Beds, Osborne Beds.

Material:

Headon Hill 2: 53 D_4, 27 P_4, 121 M_{1-2}, 47 M_3, 80 D^4, 37 P^4, 124 M^{1-2}, 50 M^3. (This list includes only teeth of which both the length and the width could be measured).

Left and right P^4, M^1 and M^2, presumably belonging to one individual.

P_4, M_1, M_2 and M_3, presumably belonging to one individual.

Fragment of upper jaw with P^4 and M^1.

Totland Bay: 31 D_4, 12 P_4, 58 M_{1-2}, 20 M_3, 36 D^4, 16 P^4, 60 M^{1-2}, 25 M^3.

Lacey's Farm Quarry (UB 6911): See Bosma and Insole (1972).

Material of *I. fordi* has also been collected from Headon Hill 3 and 4 (see section 4.2.1.6).

Measurements of the isolated cheek teeth from Headon Hill 2, Totland Bay and Lacey's Farm Quarry are given in table XVI.

Measurements of the cheek teeth in the jaw fragment from Headon Hill 2: P^4: 26.4 x 28.4; M^1: 24.9 x 30.5.

	Locality	Length				Width		
		N	range	$\bar{X}$	s	N	range	$\bar{X}$
D_4	Lacey's Farm Quarry	2	31.3–33.8	32.55	1.77	6	19.1–21.3	20.15
	Totland Bay	22	28.3–31.7	30.01	0.98	30	16.8–20.5	18.40
	Headon Hill 2	53	27.6–32.3	29.53	1.12	53	17.2–20.2	18.54
P_4	Lacey's Farm Quarry	4	28.1–31.8	30.60	1.71	4	22.2–25.6	24.20
	Totland Bay	9	27.2–31.3	29.42	1.30	,12	20.9–25.4	23.51
	Headon Hill 2	27	27.3–31.6	29.47	1.21	27	21.2–25.9	23.57
M_{1-2}	Lacey's Farm Quarry	11	22.6–28.2	25.25	1.53	11	23.6–27.9	25.50
	Totland Bay	57	23.0–28.4	25.64	1.10	56	21.2–30.3	25.50
	Headon Hill 2	121	23.0–28.4	25.70	1.05	122	23.0–29.8	25.90
M_3	Lacey's Farm Quarry	6	26.1–28.0	27.10	0.72	4	23.4–25.7	24.18
	Totland Bay	19	24.3–28.4	26.26	1.24	19	20.9–26.7	23.96
	Headon Hill 2	47	22.6–28.5	26.55	1.22	47	21.7–25.9	23.72
D^4	Lacey's Farm Quarry	8	25.9–30.3	28.56	1.43	8	23.6–26.3	24.43
	Totland Bay	34	23.3–27.7	25.85	1.20	36	20.5–24.3	22.31
	Headon Hill 2	80	23.6–27.5	25.76	0.89	80	19.4–25.1	22.71
P^4	Lacey's Farm Quarry	4	25.6–26.9	26.33	0.54	3	27.6–29.3	28.60
	Totland Bay	16	23.5–27.1	25.66	1.02	15	25.3–31.7	28.08
	Headon Hill 2	38	24.1–27.4	25.61	1.00	38	25.1–31.5	28.36
M^{1-2}	Lacey's Farm Quarry	8	22.2–23.4	22.84	0.38	6	26.7–33.3	29.32
	Totland Bay	58	21.3–25.3	23.39	0.92	57	24.5–31.4	28.44
	Headon Hill 2	125	21.2–25.1	23.43	0.82	125	25.4–33.1	28.90
M^3	Lacey's Farm Quarry	5	21.4–25.6	23.56	1.75	4	24.1–27.4	26.20
	Totland Bay	25	21.1–25.3	23.08	1.25	22	22.6–28.2	25.17
	Headon Hill 2	50	20.5–25.6	23.24	1.12	50	21.9–29.0	25.84

Table XVI. Measurements of the isolated cheek teeth of *Isoptychus fordi* Bosma and Insole, 1972 (N = number of observations, $\bar{X}$ = mean value, s = standard deviation of the sample).

Description:

In this paper we enumerate only those features that have not yet been given by Bosma and Insole (1972) in their description of *I. fordi* from Lacey's Farm Quarry, in order to illustrate the variability of the dental pattern.

D_4: The extra transverse crest present in the synclinid IV of all D_4 from Lacey's Farm Quarry (Bosma and Insole, 1972) is usually incomplete and variable in position in the D_4 from Headon Hill 2 and Totland Bay. In most specimens a cuspule or short transverse crest is present at the bottom of the sinusid. The shape of the anterior border is variable: In some D_4 it is rounded, while in others it is angular. The anterior wall shows an incision in many specimens.

P_4: The extra crest present in the synclinid IV of all P_4 from Lacey's Farm Quarry is incomplete or absent in most P_4 from Headon Hill 2 and Totland Bay. The mesolophid and ectolophid are usually complete; in some specimens these crests are interrupted. Occasional P_4 show a cingulum in the opening of the sinusid.

M_{1-2}, M_3: The molars show a simple metalophid, a metalophid of intermediate type or a complex metalophid (see section 4.2.1.1). Frequencies of the three types of metalophid in the M_{1-2} are given in table XII. The extra transverse crest that is well developed in the synclinid IV of nearly all M_{1-2} and M_3 from Lacey's Farm Quarry is variable in length and position in the M_{1-2} and M_3 from Headon Hill 2 and Totland Bay; it may even be absent. The mesolophid and ectolophid are usually complete; in some specimens they are interrupted. In one M_3 the metaconid is divided into two cusps by an incision. The width of synclinid III is variable. Incidentally a cuspule is present in the basal portion of the sinusid.

D^4: In many specimens parts of the main crests, especially of the mesoloph and the endoloph, are absent. Occasionally a small cusp is present at the lingual wall.

P^4, M^{1-2}, M^3: The P^4, M^{1-2} and M^3 have a slightly, moderately or very complex dental pattern (see section 4.2.1.1). Frequencies of the degrees of complexity of the dental pattern in the M^{1-2} are given in table X. In the P^4 the dental pattern is more complex than in the molars. The metaloph is connected with the hypocone instead of with the posteroloph in some specimens, while in others it is neither connected with the posteroloph nor with the hypocone. In some M^3 the metaloph is connected with the buccal part of the posteroloph. The buccal part of the posteroloph may be very low. The mesoloph is usually complete; it is interrupted in three M^{1-2}. Some specimens show a small cusp at their lingual wall.

Remark:

I. fordi has been described from Neustadt and Nordshausen (Fed. Rep. Germany) under the name *Thalerimys* cf. *fordi* (Tobien, 1972).

4.2.2.1.3. **Isoptychus pseudosiderolithicus** De Bonis, 1964 (Plate II, figs. 5–10; plate III, figs. 1–11)

Original reference: De Bonis (1964), p. 8–9; plate I, figs. 1–4.

Emended diagnosis:

Cheek teeth intermediate in size between those of *I. euzetensis* and *I. aquatilis.* Main cusps not very prominent. Transverse crests nearly equal in height and width.

Differential diagnosis:

I. pseudosiderolithicus differs from *I. euzetensis* in its larger cheek teeth, its less prominent main cusps and in its transverse crests that are nearly equal in height and width.

I. pseudosiderolithicus differs from *I. aquatilis* in its smaller cheek teeth.

Holotype: A fragment of a lower jaw with P_4, M_1 and M_2 (M.N.H.N. LAD 001).

Measurements cheek teeth in holotype (measured at the occlusal surface): P_4: 25.6 x 22.8; M_1 : 21.0 x 23.0; M_2: 22.8 x 24.6.

Type-locality: La Débruge (Vaucluse, France).

Stratigraphic range on the Isle of Wight: Lower Headon Beds, Upper Headon Beds, Osborne Beds, Bembridge Limestone, Bembridge Marls, Lower Hamstead Beds.

Material:

Headon Hill 2: 3 M_{1-2}, 2 D^4, 1 P^4, 5 M^{1-2}, 1 M^3.
Headon Hill 5: 1 M^{1-2}.
Lacey's Farm Quarry (UB 6911): Described by Bosma and Insole (1972) under the name *Isoptychus aquatilis.*
Headon Hill 6: 1 D_4, 1 P_4, 1 M_{1-2}, 4 D^4, 1 P^4, 6 M^{1-2}, 1 M^3.
Headon Hill 7: 2 D_4, 4 M_{1-2}, 4 M_3, 2 P^4, 3 M^{1-2}, 2 M^3.
Whitecliff Bay 2A: 1 P_4, 5 M_{1-2}, 4 M_3, 1 D^4, 2 P^4, 10 M^{1-2}, 3 M^3.
Whitecliff Bay 2B: 2 P_4, 2 M_{1-2}, 4 M_3, 3 P^4, 5 M^{1-2}, 3 M^3.
Fragment of lower jaw with D_4, M_1, M_2 and M_3.
Fragment of lower jaw with M_1 and M_2.
Fragment of upper jaw with P^4 and M^1.
Fragment of upper jaw with P^4, M^1 and M^2.
Bouldnor Cliff: 18 D_4, 43 P_4, 141 M_{1-2}, 43 M_3, 56 D^4, 36 P^4, 167 M^{1-2}, 54 M^3. (This list includes only teeth of which both the length and the width could be measured).
Fragment of lower jaw with M_1, M_2 and M_3.
Fragment of lower jaw with P_4, M_1 and incisor.
Two fragments of upper jaws with P^4 and M^1.
Material of *I. pseudosiderolithicus* has also been collected from Headon Hill 3 and 4 (see section 4.2.1.6).

	Locality	Length				Width		
		N	range	$\bar{X}$	s	N	range	$\bar{X}$
D_4	Bouldnor Cliff	15	25.5–29.4	27.20	0.95	15	15.1–17.1	16.09
	Headon Hill 7	2	26.8–27.2	27.00	0.28	1	–	16.0
	Headon Hill 6	1	–	26.3	–	1	–	14.9
	Lacey's Farm Quarry	4	26.5–27.3	26.95	0.41	7	13.4–16.1	15.09
P_4	Bouldnor Cliff	33	23.1–28.3	25.69	1.23	33	17.4–22.0	19.11
	Whitecliff Bay 2B	–	–	–	–	2	18.7–20.1	19.40
	Whitecliff Bay 2A	–	–	–	–	1	–	19.5
	Headon Hill 6	1	–	23.7	–	–	–	–
	Lacey's Farm Quarry	1	–	22.9	–	5	16.8–18.9	17.94
M_{1-2}	Bouldnor Cliff	117	18.8–23.6	21.39	1.10	117	17.1–27.5	20.13
	Whitecliff Bay 2B	2	20.7–20.8	20.75	0.07	1	–	21.9
	Whitecliff Bay 2A	5	19.7–22.2	20.74	0.98	5	19.7–23.3	21.60
	Headon Hill 7	4	20.1–20.6	20.38	0.22	3	19.2–23.6	21.70
	Headon Hill 6	1	–	21.2	–	–	–	–
	Lacey's Farm Quarry	21	18.5–22.6	20.16	1.01	21	17.0–20.9	19.10
	Headon Hill 2	3	20.4–21.5	21.07	0.59	3	18.7–19.5	19.07
M_3	Bouldnor Cliff	34	19.1–24.9	22.01	1.28	34	17.1–21.4	19.22
	Whitecliff Bay 2B	3	21.2–22.1	21.57	0.47	3	17.8–19.3	18.57
	Whitecliff Bay 2A	4	20.0–22.2	20.75	1.01	4	16.9–19.3	18.13
	Headon Hill 7	4	20.2–24.6	22.75	1.87	4	18.5–19.5	18.98
	Lacey's Farm Quarry	3	20.6–22.9	21.67	1.16	1	–	18.5
D^4	Bouldnor Cliff	48	21.0–25.1	23.33	0.94	48	16.7–21.4	18.92
	Whitecliff Bay 2A	–	–	–	–	1	–	17.8
	Headon Hill 6	2	22.2–24.9	23.55	1.91	3	19.0–21.5	20.27
	Lacey's Farm Quarry	3	21.0–22.0	21.63	0.55	5	17.3–18.7	17.90
	Headon Hill 2	2	20.4–21.0	20.70	0.42	2	16.8–18.8	17.80
P^4	Bouldnor Cliff	26	18.8–23.4	21.23	1.03	26	20.5–27.6	24.01
	Whitecliff Bay 2B	3	20.7–21.9	21.20	0.62	3	22.2–24.4	23.17
	Whitecliff Bay 2A	2	20.8–22.2	21.50	0.99	2	22.0–22.2	22.10
	Headon Hill 7	2	19.8–22.5	21.15	1.91	2	23.9–24.4	24.15
	Headon Hill 6	1	–	21.5	–	–	–	–
	Lacey's Farm Quarry	1	–	20.8	–	4	20.5–22.4	21.78
	Headon Hill 2	1	–	20.2	–	1	–	21.6
M^{1-2}	Bouldnor Cliff	157	16.7–22.5	19.75	1.07	157	19.5–28.1	22.79
	Whitecliff Bay 2B	5	17.0–20.9	18.84	1.71	5	21.5–23.9	22.70
	Whitecliff Bay 2A	10	17.8–20.4	19.04	0.89	6	21.8–25.9	23.35
	Headon Hill 7	3	17.4–18.9	18.27	0.78	3	21.9–25.4	23.77
	Headon Hill 6	6	17.4–19.6	18.65	0.88	6	21.6–25.3	23.13
	Lacey's Farm Quarry	19	17.7–21.2	18.72	1.03	17	20.2–24.3	22.43
	Headon Hill 5	1	–	18.9	–	1	–	25.4
	Headon Hill 2	5	18.2–20.0	19.14	0.73	5	22.4–23.3	22.92
M^3	Bouldnor Cliff	54	16.6–21.1	19.00	0.97	54	18.6–24.8	21.01
	Whitecliff Bay 2B	2	17.6–18.6	18.10	0.71	2	20.3–22.2	21.25
	Whitecliff Bay 2A	3	18.7–20.0	19.23	0.68	3	20.2–21.8	21.00
	Headon Hill 7	2	18.2–19.0	18.60	0.57	2	20.3–22.2	21.25
	Headon Hill 6	1	–	19.4	–	1	–	22.1
	Lacey's Farm Quarry	8	15.8–19.3	17.74	1.13	5	18.3–21.7	20.14

Measurements of the isolated cheek teeth from Headon Hill 2 and 5, Lacey's Farm Quarry, Headon Hill 6 and 7, Whitecliff Bay 2A and B, and Bouldnor Cliff are given in table XVII.

Measurements of the cheek teeth in the jaw fragments:

Whitecliff Bay 2B: D_4: – x 15.2; M_1: 20.3 x 20.5; M_2: 20.5 x 21.2; M_3: – x –.

M_1: 21.2 x 18.1; M_2: 23.8 x 20.5.

P^4: 19.1 x 20.8; M^1: 17.2 x 21.8.

P^4: 22.0 x 22.6; M^1: 21.5 x 23.5; M^2: 21.6 x 25.4.

Bouldnor Cliff: M_1: 22.0 x 21.2; M_2: 21.8 x 22.4; M_3: 22.1 x 20.8.

P_4: 31.9 x 24.2; M_1: 25.7 x 24.6.

P^4: 21.3 x 22.6; M^1: 19.7 x 25.4.

P^4: 19.5 x 21.2; M^1: 22.2 x 22.6.

Description:

D_4: The deciduous teeth are less hypsodont than the permanent ones. Moreover, their pattern is more complicated; yet the main cusps and crests can be clearly distinguished. All specimens show a short crest extending from the lingual end of the mesolophid into synclinid III. The mesolophid is usually complete; only in one D_4 it is interrupted in the middle.

P_4: The dental pattern is simple, although small extra cusps and crests may be present. Synclinid II is U-shaped. The mesolophid is usually complete; its lingual part is absent in two specimens. Crests of variable height frequently extend from the middle or the lingual end of the mesolophid into synclinid III. One P_4 shows a cingulum in the opening of the sinusid.

M_{1-2}, M_3: The dental pattern is little complex, although small additional cusps and crests occur. The metalophid in some specimens shows a slight antero-buccal swelling, which may cause a small inward fold of the metalophid. This fold may be accompanied by an anterior accessory cuspule of variable size, which does not reach the occlusal surface. Both fold and cuspule soon disappear by attrition. In some specimens a short crest extends from the metaconid in front of the metalophid in buccal direction. This crest may be connected with the middle of the metalophid, delimiting a synclinid I. In one M_3 the metalophid is completely double, consisting of an anterior and a posterior branch. Two extra connections are present between these branches. The mesolophid is usually complete; in some teeth it is interrupted and in one M_3 it is even absent. In the M_3 figured on plate III, fig. 5 and in another M_3 the posterolophid is partly represented by a cusp. In a third M_3 the lingual part of the posterolophid shows a small inward fold. The width of synclinid III is variable. In one M_{1-2} synclinid III is closed lingually by a high crest.

Table XVII. Measurements of the isolated cheek teeth of *Isoptychus pseudosiderolithicus* De Bonis, 1964 (N = number of observations, $\bar{X}$ = mean value, s = standard deviation of the

D^4: The milk teeth are less hypsodont than the (pre)molars. The dental pattern is relatively complex, showing a number of additional crests and cuspules. Yet the main cusps and crests can be clearly distinguished. The mesoloph is complete in most specimens; only in three D^4 it is incomplete. The endoloph may be interrupted at the posterior side of the protocone. In occasional specimens the lingual connection between the metaloph and the posteroloph is interrupted. Most D^4 show a sixth transverse crest, which is situated in syncline I. This extra crest and the anteroloph delimit an extra syncline.

P^4, M^{1-2}, M^3: The dental pattern shows little complication. Small additional cusps and crests may occur. Syncline IV can be usually recognized in very worn teeth also. The mesoloph is complete in most specimens; it may be interrupted lingually, in the middle or buccally. In some specimens the lingual connection between metaloph and posteroloph is interrupted. In one P^4 and one M^3 the metaloph is connected with the hypocone instead of with the posteroloph. In another P^4 and in some other M^3 the buccal part of the posteroloph is absent; consequently, syncline IV is nearly absent in these specimens. Incidentally the endoloph is interrupted at the posterior side of the protocone. In some specimens syncline III is considerably longer than synclines I and II.

Lower jaw: The intersection of the coronoid and angular crests is situated below the anterior part or the middle of the M_1. A prominent horizontal ledge extends from this intersection in forward direction to a point below the middle of the P_4.

Upper jaw (see also section 4.2.2.1.1): The posterior border of the incisive foramen is situated in line with the posterior half of the P^4 (Plate II, fig. 5).

Discussion:

Many cheek teeth of *I. pseudosiderolithicus* from the Isle of Wight are slightly smaller than those of *I. pseudosiderolithicus* from the type-locality. Nevertheless, the assemblages from the Isle of Wight are referred to as *I. pseudosiderolithicus,* because of the conformity in dental structure. The English material shows similarity in size to *I. euzetensis,* but most of the cheek teeth from the Isle of Wight differ from those of *I. euzetensis* in showing less prominent main cusps, a less prominent metalophid, entolophid, protoloph and metaloph, and a more prominent mesolophid and mesoloph. Moreover, the lower molars seem to be higher crowned and frequently show an anteroconid. On the other hand, a few specimens of *I. pseudosiderolithicus* from the Isle of Wight are indistinguishable from those of *I. euzetensis. I. pseudosiderolithicus* from the Isle of Wight is considerably smaller than *I. aquatilis* from its type-locality, Ronzon (France).

I. pseudosiderolithicus is also known from Hoogbutsel and Hoeleden (Belgium) and Neustadt (Fed. Rep. Germany), under the name *Theridomys aquatilis* (Misonne, 1957; Vianey-Liaud, 1972c; Tobien, 1972). The cheek teeth from the Isle of Wight and Hoogbutsel are similar in size and in pattern.

The fragment of a lower jaw with P_4 and M_1 from Bouldnor Cliff has been included in *I. pseudosiderolithicus.* Because of the large size of the P_4 and M_1 it might be referred to as *I. aquatilis.*

It cannot be excluded that the assemblages of *I. pseudosiderolithicus* incidentally comprise molars of *Pseudoltinomys gaillardi* (Stehlin and Schaub, 1951), since specimens of *Isoptychus* and *Pseudoltinomys* Lavocat, 1951 may resemble closely (see also section 4.2.3.1.1).

4.2.3. Subfamily ISSIODOROMYINAE Lavocat, 1951

4.2.3.1. Genus **Pseudoltinomys** Lavocat, 1951

Original reference: Lavocat (1951), p. 53, p. 78.
Type-species: Theridomys (Oltinomys) gaillardi Stehlin and Schaub, 1951.

Emended diagnosis:

Issiodoromyinae with slightly hypsodont cheek teeth. Most lower molars provided with an antesinusid. Sinus and syncline II usually confluent. Premolars and milk molars small compared to the molars. Incisors laterally compressed.

Differential diagnosis:

Pseudoltinomys differs from *Oltinomys* in its higher-crowned cheek teeth and in the structure of the palate; in *Pseudoltinomys* the incisive foramen extends to close to the premolar.

4.2.3.1.1. **Pseudoltinomys gaillardi** (Stehlin and Schaub, 1951) (Plate IV, figs. 3–7)

Original reference: Theridomys (Oltinomys) gaillardi Stehlin and Schaub, 1951; p. 216, p. 363.

Diagnosis:

A species of *Pseudoltinomys* with cheek teeth in which the transverse crests are subequal in height and thickness, and in which the main cusps are not very prominent.

Holotype: A fragment of a skull with left and right P^4–M^3 (F.S.L. R38).

Type-locality: Ronzon (Haute-Loire, France).

Stratigraphic range on the Isle of Wight: Lower Hamstead Beds. The presence of *Pseudoltinomys* in the Osborne Beds, and the species assignments of *Pseudoltinomys* from the Upper Headon Beds, Bembridge Limestone and Bembridge Marls are not certain (see Discussion).

Material:
Headon Hill 3: 4 M_{1-2}, 1 M^{1-2}.
Whitecliff Bay 2B: 1 M^{1-2}.
Bouldnor Cliff: 3 P_4, 8 M_{1-2}, 2 M_3, 2 D^4, 1 P^4, 4 M^{1-2}, 1 M^3.
A fragment of a M_{1-2} from Headon Hill 7 indicates the presence of *Pseudoltinomys* in the Bembridge Limestone.

Measurements: see table XVIII.

Description:

P_4: The lingual part of the posterolophid is low. The anterior wall of one specimen is curved inward (Plate IV, fig. 3).

	Locality	Length				Width		
		N	range	$\bar{X}$	s	N	range	$\bar{X}$
P_4	Bouldnor Cliff	3	19.3–21.1	20.40	0.96	3	14.9–16.1	15.43
M_{1-2}	Bouldnor Cliff	8	18.2–20.2	19.59	0.86	8	15.2–18.3	16.94
	Headon Hill 3	4	19.6–21.4	20.68	0.76	4	17.8–19.4	18.83
M_3	Bouldnor Cliff	2	21.4–24.0	22.70	1.84	2	17.9–18.7	18.30
D^4	Bouldnor Cliff	2	15.8–17.5	16.65	1.20	2	15.2–16.5	15.85
P^4	Bouldnor Cliff	1	–	17.1	–	1	–	20.2
M^{1-2}	Bouldnor Cliff	4	17.2–18.8	17.85	0.72	4	17.3–21.2	19.53
	Whitecliff Bay 2B	1	–	20.7	–	–	–	–
	Headon Hill 3	1	–	19.8	–	1	–	21.8
M^3	Bouldnor Cliff	1	–	19.3	–	1	–	18.4

Table XVIII. Measurements of the cheek teeth of *Pseudoltinomys gaillardi* (Stehlin and Schaub, 1951) (N = number of observations, $\bar{X}$ = mean value, s = standard deviation of the sample).

M_{1-2}, M_3: The mesolophid is often slightly lower than the metalophid and the entolophid, and may be incomplete (Plate IV, fig. 4). The aperture of synclinid III is very wide in some specimens. The metalophid and the mesolophid connect lingually in some teeth, but are separated in others. The thickness of the individual transverse crests is variable. In both M_3 a crest extends from the metaconid in antero-buccal direction; this crest is connected to the middle of the metalophid, delimiting a synclinid I, in one of these two specimens.

D^4: The deciduous teeth are low crowned. Five transverse crests are present. In both specimens the sinus and syncline II are separated by an indistinct crest. The occlusal surface is slightly concave.

P^4: In the single P^4 the paracone and metacone are relatively high. The buccal parts of the anteroloph and posteroloph are low. The posteroloph shows an inward curve, close to the hypocone. The mesoloph is relatively narrow. Syncline I is short, as the protoloph is connected to the anteroloph instead of to the protocone. The metaloph and posteroloph are not connected.

M^{1-2}: Syncline IV is well developed. The occlusal surface is slightly concave. The single M^{1-2} from Headon Hill 3 differs from the other M^{1-2} in that its paracone is large, the mesoloph is narrow, the metaloph and posteroloph are not connected lingually, the mesoloph shows an angle at the junction of the sinus and syncline II. The latter feature is also present in the M^{1-2} from Whitecliff Bay 2B.

M^3: In the only M^3 available the buccal part of the posteroloph is low. Yet syncline IV is well developed.

Discussion:

The assemblages of *Isoptychus pseudosiderolithicus* De Bonis, 1964 may incidentally comprise molars of *Pseudoltinomys,* because the ranges of variation of the molars of *Isoptychus* Pomel, 1853 and *Pseudoltinomys* overlap. The M_{1-2} B.U. 20671 from Lacey's Farm Quarry has been placed in *I. pseudosiderolithicus* (see section 4.2.2.1.3 and Bosma and Insole, 1972), but its small antesinusid and rather wide aperture of synclinid III may indicate that *Pseudoltinomys* is present in the Osborne Beds.

Besides, a correct determination of our material is complicated by the uncertainty with regard to the distinction between *P. gaillardi* and *P. cuvieri* (Pomel, 1853). *P. cuvieri* from the type-locality Montmartre (France) is only known by its holotype, a fragment of a lower jaw with D_4–M_3 (M.N.H.N. no. A.C. 1339). This specimen differs from *P. gaillardi* in the slightly lower-crowned cheek teeth and in the slightly lower mesolophid. Three out of four

M_{1-2} from Headon Hill 3 resemble *P. cuvieri* regarding the latter characteristic.

The *Pseudoltinomys* material from Headon Hill 3 and 7, and Whitecliff Bay 2B is provisionally assigned to *P. gaillardi,* because of lack of sufficient material from these localities. By way of precaution, *Pseudoltinomys* from localities other than Bouldnor Cliff are indicated as *Pseudoltinomys* sp. in the range and correlation charts (text-figs. 37 and 38).

Remarks:

In addition to the type-locality, *P. gaillardi* has been recorded from Montalban, Spain (Thaler, 1969), Mège and Pech-Crabit, Quercy, France (Vianey-Liaud, 1969), Fontaines-de-Vaucluse, Vaucluse, France (Helmer and Vianey-Liaud, 1970) and Malemort, Vaucluse, France (Triat, Truc and Hugueney, 1971), occasionally as *P.* aff. *gaillardi.* The associated faunas from these localities suggest a considerable range in age. Consequently, *P. gaillardi* cannot be used for detailed stratigraphical correlation.

4.2.4. Subfamily OLTINOMYINAE Hartenberger, 1971

4.2.4.1. Genus Ectropomys Bosma and Schmidt-Kittler, 1972

Original reference: Bosma and Schmidt-Kittler (1972), p. 185.
Type-species: Ectropomys exiguus Bosma and Schmidt-Kittler, 1972.

4.2.4.1.1. **Ectropomys exiguus** Bosma and Schmidt-Kittler, 1972

Original reference: Bosma and Schmidt-Kittler (1972), p.185–186; plate I, figs. 1–11.

Holotype: An isolated M^{1-2} (G.I.U. WB2B 101).

Type-locality: Whitecliff Bay 2B (Isle of Wight, England).

Stratigraphic range on the Isle of Wight: Bembridge Limestone, Bembridge Marls.

Discussion:

E. exiguus has been collected from Headon Hill 7 and Whitecliff Bay 2A and B. The material has been described by Bosma and Schmidt-Kittler (1972). These authors showed that the species is also present in the fissure fillings Ehrenstein 1 (A), Weissenburg 8 and Möhren 6 (Fed. Rep. Germany).

4.3. Family CRICETIDAE Rochebrune, 1883

Subfamily EUCRICETODONTINAE Mein and Freudenthal, 1971

4.3.1. Genus **Eucricetodon** Thaler, 1966

Original reference: Thaler (1966), p. 140–141.
Subsequent reference: Vianey-Liaud (1972a), p. 4.
Type-species: Cricetodon collatum Schaub, 1925.

4.3.1.1. **Eucricetodon atavus** (Misonne, 1957) (Plate IV, figs. 8–9)

Original reference: Cricetodon atavus Misonne, 1957; p. 7–8; plate II, figs. 4–6.
Subsequent reference: Vianey-Liaud (1972a), p. 6.

Holotype: An isolated M^1 (I.S.B. Ctm 1146).

Type-locality: Hoogbutsel (Belgium).

Stratigraphic range on the Isle of Wight: Lower Hamstead Beds.

Material and measurements:
Bouldnor Cliff: 1 M^1 (17.7 x 12.1) (Plate IV, fig. 8); 1 M^2 (13.3 x 13.0) (Plate IV, fig.9).

Description:

M^1: The anterocone is one single cusp; its posterior wall is situated close to the protolophule I. The protolophule I is higher than the protolophule II. A mesoloph is hardly developed. The metaloph is connected with the anterior part of the hypocone.

M^2: The protolophule II is low. The endoloph is constricted in the middle.

Remarks:

In addition to the type-locality, *E. atavus* is known from Malemort (Vaucluse, France) (Triat, Truc and Hugueney, 1971), Montalban (Spain), Aubrelong, Mège, Pech-Crabit and Mas de Got (Quercy, France), and Les Chapelins (Vaucluse, France) (Vianey-Liaud, 1972a), occasionally as *E.* cf. *atavus.*

4.4. Family CASTORIDAE Gray, 1821

Genus Steneofiber Geoffroy, 1833

Type-species: Steneofiber castorinus Pomel, 1846.
Diagnosis: See Stehlin and Schaub (1951), p. 62–65, p. 223–225.

4.4.1. Steneofiber sp. (Plate IV, figs. 1a–b and 2)

Stratigraphic range on the Isle of Wight: Lower Hamstead Beds.

Material:
Bouldnor Cliff: Fragment of a lower jaw with P_4 (B.M.(N.H.) M19207).
Bouldnor Cliff ?: Fragment of a lower jaw with P_4–M_1 (B.M.(N.H.)M14748).

Measurements:
B.M.(N.H.) M19207: P_4: 50.5 x 42.5.
B.M.(N.H.) M14748: P_4: –x 40.0; M_1 : 39.0 x 39.0.

Description:
All teeth are rather worn. The P_4 of M19207 (Plate IV, fig. 2) shows the synclinids I–IV. Only the transverse synclinid III is open lingually. Synclinid I is L-shaped; it is only just closed antero-buccally. Synclinid II is small and rounded. The upper part of the anterior wall shows a slight inward curve. The P_4 of M14748 (Plate IV, fig. 1b) shows the synclinids I, III and IV. All synclinids are closed lingually. Synclinid I is L-shaped. It is open antero-buccally. Synclinid IV is divided into two parts. The buccal parts of synclinid IV and synclinid III are situated close together.

The M_1 (Plate IV, fig. 1b) shows three synclinids (I or II, III and IV). Only synclinid III is open lingually. The occlusal surface of all teeth is flat.

The coronoid crest is prominent and terminates below the posterior part of the M_1 (Plate IV, fig. 1a).

Discussion:
Steneofiber from Bouldnor Cliff could not be determined specifically, because of the absence of upper cheek teeth and the advanced stage of wear of the lower cheek teeth, which prevents the observation of details of the occlusal surface. The teeth show some similarity in pattern to those of *Steneofiber butselensis* (Misonne, 1957) from Hoogbutsel (Belgium), but they are slightly longer and wider.

4.5. Family PARAMYIDAE Miller and Gidley, 1918

Subfamily MANITSHINAE Simpson, 1941

Genus **Plesiarctomys** Bravard

Early reference: Gervais (1848–1852), t. II, explanation of plate 46, p. 2; t. III, plate 46, fig. 13.
Subsequent reference: Wood (1970), p. 241–242.
Type-species: Plesiarctomys gervaisii Gervais, 1848–1852.

4.5.1. **Plesiarctomys** sp. (Plate IV, fig. 10)

Material:
Headon Hill 1: 1 M^{1-2} (probably M^2).

Measurements: 36.8 x 42.9.

Description:
A very worn tooth with distinct paracone, metacone, hypocone, protoconule, metaconule and mesostyle. The protocone is indistinct. Minor crests connect the protoconule and the metaconule with the anterior and posterior parts of the protocone respectively. The mesostyle is closely connected with the paracone; it extends into the central valley as a short crest. A cuspule is present between the mesostyle and the metacone. The anteroloph is slightly enlarged in front of the protocone. The lingual wall shows a slight depression between the protocone and the hypocone. The occlusal surface is strongly concave.

The tooth is probably a M^2, as it is rather rectangular, while the metacone separates the posteroloph from the buccal margin of the tooth (cf. Wood, p. 247).

Discussion:
The specimen might belong to *P. hartenbergeri* Wood, 1970 or to *P. spectabilis* (Major, 1873). Its pattern resembles that of the M^{1-2} of both species, because the hypocone is well developed and because the anteroloph is enlarged in front of the protocone. The difference in size between *P. hartenbergeri* and *P. spectabilis* is small. The assignment of the tooth from Headon Hill 1 to one of these two species would therefore require more material. The specimen is distinctly smaller than the M^{1-2} of *P. hurzeleri* Wood, 1970 and *P. gervaisi.*

P. hartenbergeri and *P. spectabilis* are known from the Middle Eocene localities Bouxwiller (Alsace, France), Egerkingen and Chamblon (Switzerland). These species are much older than *Plesiarctomys* from Headon Hill 1. *P. hurzeleri* and *P. gervaisi* have been collected from Robiac (Gard, France), La Débruge (Vaucluse, France), Euzet (Gard, France) and various localities in Switzerland and Quercy, France (see Wood). The associated faunas indicate that these localities are of approximately the same age as Headon Hill 1 or slightly older (Robiac).

It may be concluded that at least three species of *Plesiarctomys,* which show amongst other things considerable difference in size, can be expected in Late Eocene localities.

Chapter 5

BIOSTRATIGRAPHY

5.1. Introduction.

The position of the sampled localities relative to the lithostratigraphic sequence, which is partly clear from their field position (HH1-7, TB, BC) and partly interpreted from the general lithostratigraphic situation (WB1, WB2A and B, LFQ), forms the basis of the sequence of rodent associations illustrated in the distribution diagram (text-fig. 37). From this sequence a number of biozones can be inferred.

This procedure, commonly in use in invertebrate biostratigraphy, has rarely been applied to mammalian biostratigraphy. This is largely due to the circumstance that mammal associations are often collected from localities that show no clear mutual lithostratigraphic relations.

5.2. Biozonation.

The following zones (text-fig. 38) can be recognized from below upwards:

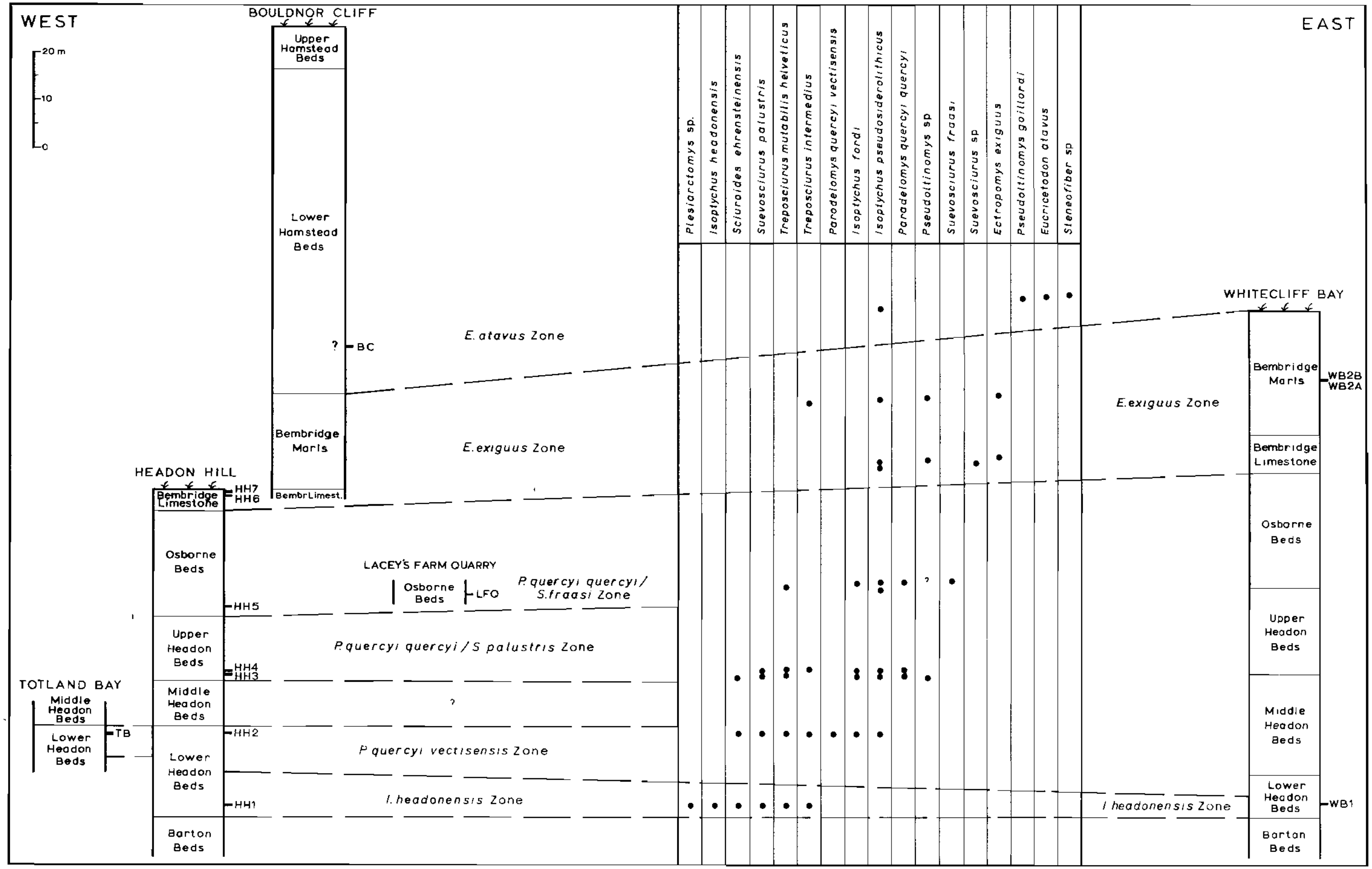
1. The *Isoptychus headonensis* Zone.
   Diagnosis: Characterized by the total range of *I. headonensis.*
   Additional fauna observed: *Plesiarctomys* sp., *Sciuroides ehrensteinensis, Suevosciurus palustris, Treposciurus mutabilis helveticus* and *Treposciurus intermedius.*
   Type-locality: Headon Hill 1 (Isle of Wight, England).
   Type-level: Lower part Lower Headon Beds.
   Other locality: Whitecliff Bay 1.

2. The *Paradelomys quercyi vectisensis* Zone.
   Diagnosis: Characterized by the total range of *P. quercyi vectisensis.*
   Additional fauna observed: *Sciuroides ehrensteinensis, Suevosciurus palustris, Treposciurus mutabilis helveticus, Treposciurus intermedius, Isoptychus fordi* and *Isoptychus pseudosiderolithicus.*
   Type-locality: Headon Hill 2 (Isle of Wight, England).
   Type-level: Upper part Lower Headon Beds.
   Other locality: Totland Bay.

SPECIES \ LOCALITIES	HEADON HILL 1	WHITECLIFF BAY 1	HEADON HILL 2	TOTLAND BAY	HEADON HILL 3	HEADON HILL 4	HEADON HILL 5	LACEY'S FARM QUARRY	HEADON HILL 6	HEADON HILL 7	WHITECLIFF BAY 2A	WHITECLIFF BAY 2B	BOULDNOR CLIFF
Plesiarctomys sp.	•												
Isoptychus headonensis	•	•											
Sciuroides ehrensteinensis	•		•	•	•								
Suevosciurus palustris	•		•	•	•	•							
Treposciurus mutabilis helveticus	•		•	•	•	•		•					
Treposciurus intermedius	•		•			•					•		
Paradelomys quercyi vectisensis			•	•									
Isoptychus fordi			•	•	•	•		•					
Isoptychus pseudosiderolithicus			•		•	•	•	•	•	•	•	•	•
Paradelomys quercyi quercyi					•	•		•					
Pseudoltinomys sp					•			?		•		•	
Suevosciurus fraasi								•					
Suevosciurus sp.									•				
Ectropomys exiguus										•	•	•	
Pseudoltinomys gaillardi													•
Eucricetodon atavus													•
Steneofiber sp.													•

BIOZONES	HEADON HILL 1	WHITECLIFF BAY 1	HEADON HILL 2	TOTLAND BAY	HEADON HILL 3	HEADON HILL 4	HEADON HILL 5	LACEY'S FARM QUARRY	HEADON HILL 6	HEADON HILL 7	WHITECLIFF BAY 2A	WHITECLIFF BAY 2B	BOULDNOR CLIFF
Isoptychus headonensis Zone	—	—											
Paradelomys quercyi vectisensis Zone			—	—									
Paradelomys quercyi quercyi / Suevosciurus palustris Zone					—	—							
Paradelomys quercyi quercyi / Suevosciurus fraasi Zone								—					
Ectropomys exiguus Zone										—	—	—	
Eucricetodon atavus Zone													—

Text-fig. 37 Range chart of rodent associations, with localities and rodent zones. Data on the Rodentia from Lacey's Farm Quarry other than those on *I. fordi* Bosma and Insole, 1972 and *I. pseudosiderolithicus* De Bonis, 1964 have been made available by Dr. A. N. Insole, Bristol.



Text-fig. 38 Correlation chart of rodent zones and formations in the sections at Headon Hill, Totland Bay, Bouldnor Cliff, Lacey's Farm Quarry and Whitecliff Bay.

3. The *Paradelomys quercyi quercyi-Suevosciurus palustris* Zone.
Diagnosis: Characterized by the concurrent range of *P. quercyi quercyi* and *S. palustris. P. quercyi quercyi:* entry Headon Hill 3, exit Lacey's Farm Quarry; *S. palustris:* entry Headon Hill 1, exit Headon Hill 4.
Additional fauna observed: *Sciuroides ehrensteinensis, Treposciurus mutabilis helveticus, Treposciurus intermedius, Isoptychus fordi, Isoptychus pseudosiderolithicus* and *Pseudoltinomys* sp.
Type-locality: Headon Hill 3 (Isle of Wight, England).
Type-level: Upper Headon Beds.
Other locality: Headon Hill 4.

4. The *Paradelomys quercyi quercyi-Suevosciurus fraasi* Zone.
Diagnosis: Characterized by the concurrent range of *P. quercyi quercyi* and *S. fraasi.*
Additional fauna observed: *Treposciurus mutabilis helveticus, Isoptychus fordi, Isoptychus pseudosiderolithicus* and possibly *Pseudoltinomys* sp.
Type-locality: Lacey's Farm Quarry (University of Bristol site no. 6911) (Isle of Wight, England).
Type-level: Osborne Beds.
Remark: The position of sample HH5 is uncertain, as its fauna only contains *I. pseudosiderolithicus.*

5. The *Ectropomys exiguus* Zone.
Diagnosis: Characterized by the total range of *E. exiguus.*
Additional fauna observed: *Treposciurus intermedius, Isoptychus pseudosiderolithicus* and *Pseudoltinomys* sp.
Type-locality: Headon Hill 7 (Isle of Wight, England).
Type-level: Top part Bembridge Limestone (see section 3.2.1).
Other localities: Whitecliff Bay 2A and B.
Remark: The position of sample HH6 is uncertain, as its fauna consists of *Isoptychus pseudosiderolithicus* and *Suevosciurus* sp. only. The field position of Headon Hill 6 is close to that of Headon Hill 7.

6. The *Eucricetodon atavus* Zone.
This zone is provisional, as its upward extension is uncertain. On the Isle of Wight the interval is very characteristic, because it includes the first primitive representatives of the Cricetidae *(E. atavus)* and the Castoridae (*Steneofiber* sp.). The only certain element from older levels is *Isoptychus pseudosiderolithicus.* It is possible that *Pseudoltinomys gaillardi* may also be present in older levels (see section 4.2.3.1.1).
Type-locality: Bouldnor Cliff (Isle of Wight, England).
Type-level: Lower Hamstead Beds.

5.3. Correlation with earlier established biostratigraphic units.

Comparison of our zonation with the only other zonation given in this stratigraphic interval, that of Thaler (1966), is somewhat obfuscated by the difference in approach towards the establishment of zones. The only zone of Thaler that can be directly compared to our sequence is the "zone" of Montmartre. This zone is characterized by the presence of *Isoptychus auberyi* Pomel, 1853 (nomen nudum = *I. pseudosiderolithicus* De Bonis, 1964). However, the range of *I. pseudosiderolithicus* covers five of our zones (see text-fig. 37).

Stehlin (1909) and Depéret (1917) considered the mammalian fauna from Hordle Cliff (Hampshire), which locality is also situated in the Hampshire Basin, to be of the same age as the fauna from Euzet (France); Franzen (1968) considered the fauna from Hordle Cliff to be slightly older than the fauna from Euzet. The fauna from Hordle Cliff contains *Isoptychus headonensis,* marker for our *I. headonensis* Zone. This concurs very well with the succession usually accepted for the "zones" of Euzet and Montmartre.

5.4. Correlation with localities outside England that are interrelated with marine deposits.

1. *Hoogbutsel* (Belgium).

The mammalian fauna from Bouldnor Cliff (Lower Hamstead Beds, *Eucricetodon atavus* Zone) shows close resemblance to the fauna from Hoogbutsel. The sediment of the locality of Hoogbutsel is the type-deposit of the Horizon of Hoogbutsel defined by Glibert and De Heinzelin (1952). This member has been situated in between the Sands of Neerrepen and the Sands of Boutersem and has been placed at the base of the Upper Tongrian (Denizot, 1957).

The degree of similarity of the rodent associations from Bouldnor Cliff and Hoogbutsel is shown in the following list:

	Bouldnor Cliff	Hoogbutsel
Isoptychus pseudosiderolithicus	x	x
Pseudoltinomys gaillardi	x	
Suevosciurus palustris		x
Eucricetodon atavus	x	x
Steneofiber butselensis		x
Steneofiber sp.	x	
Eomyid		x

This list does not include the Gliridae, which will be the subject of a later paper.

Similarity of the rodent faunas from Bouldnor Cliff and Hoogbutsel is mainly suggested by the presence of primitive species of the Cricetidae and the Castoridae at both localities. *Isoptychus pseudosiderolithicus* predominates in Bouldnor Cliff as well as in Hoogbutsel.

The presence of *Suevosciurus palustris* in Hoogbutsel is not in accordance with the suggested correlation. On the Isle of Wight this species has been collected from the lower levels of Headon Hill 1 and 2, Totland Bay and Headon Hill 3 and 4. A larger species, *S. fraasi,* is known from Lacey's Farm Quarry (Insole, 1972), which level is still two zones lower than Bouldnor Cliff. Species of the genus *Suevosciurus* are thought to be extremely useful for stratigraphical correlation because of their general increase in size. The similarity in size between the *Suevosciurus* species from Hoogbutsel and that from the Headon Beds thus would suggest that the fauna of Hoogbutsel is considerably older than that of Bouldnor Cliff. This conclusion, however, is opposed by the absence of species of the Cricetidae and the Castoridae in the Lower and Upper Headon Beds, and by the absence of *Isoptychus fordi* and Pseudosciuridae other than *Suevosciurus palustris* in Hoogbutsel. Alternatively, the presence of two *Suevosciurus* lineages may solve the problem. *S. palustris* from Headon Hill 1 and 2, Totland Bay and Headon Hill 3 and 4 would be members of the *Suevosciurus* lineage consisting of large forms, whereas *S. palustris* from Hoogbutsel would belong to the other *Suevosciurus* lineage, which comprises the smaller forms (see section 4.1.2.1).

Similarity of the non-rodent mammalian faunas from Bouldnor Cliff and Hoogbutsel is demonstrated by the presence of the insectivore *Butselia biveri* Quinet and Misonne, 1965 at both localities (Butler, 1972). This species is up till now unknown from other localities.

As a whole, the Horizon of Hoogbutsel is thought to correspond to our *E. atavus* Zone.

2. *Neustadt and Nordshausen* (Fed. Rep. Germany).

The Melanienton of Northern Hesse has yielded faunas of micromammals near Neustadt and Nordshausen. Rodents form part of these faunas (Tobien, 1971 and 1972). The presence of *Isoptychus pseudosiderolithicus, Isoptychus fordi* and *Suevosciurus palustris* (called *Theridomys (Theridomys) aquatilis, Thalerimys* cf. *fordi* and *Suevosciurus fraasi* respectively by Tobien) indicates similarity in age between the faunas from Neustadt and Nordshausen on the one hand, and the faunas from Headon Hill 2, Totland Bay and Headon Hill 3 and 4 (*Paradelomys quercyi vectisensis* Zone and *Paradelomys quercyi quercyi-Suevosciurus palustris* Zone) on the other.

Chapter 6

CHRONOSTRATIGRAPHY

6.1. The Headonian –a proposed new stage.

In the Eocene and Oligocene the stages are usually based on stratotypes in more or less marine sequences. It is a current procedure that such stage names are applied to non-marine sequences as well, which strata often have no immediately recognizable connection with marine deposits. The stage name Ludian, for instance, is regularly used in connection with the mammalian faunas of Euzet and Hordle Cliff, while the faunas from Bouldnor Cliff, Hoogbutsel and Ronzon are usually placed in the Sannoisian. However, the localities can hardly be correlated with marine sequences.

In our opinion it is preferable to use different systems of chronostratigraphic terms for continental and marine successions. Therefore, it is proposed to use a new stage name in the continental chronostratigraphic system, the Headonian, which is based on our data. It is, of course, advisable to link the two chronostratigraphic systems, but geological conditions making this possible are as yet scarce and by no means fully exploited. It will be shown that, to a certain extent, the interrelation between the continental and marine chronostratigraphic systems may be attempted in the Isle of Wight sections.

HEADONIAN

1. Stage name: Headonian.
2. Designation stratotype: Headon Hill section (text-figs. 6 and 7).
3. Geographic description: The stratotype is formed by the western seaward face of the cliff at Headon Hill (Nat. Grid Ref. SZ 305858).
4. Geological description of the stratotype: The type Headonian comprises the predominantly continental deposits of the Paleogene succession at Headon Hill. The following formations are recognized in regular superposition:

Osborne Beds
Upper Headon Beds
Middle Headon Beds (marine)
Lower Headon Beds

4.1. Lithologic description: See Forbes (1853, 1856), Bristow, Reid and Strahan (1889), White (1921), Curry (1958), Chatwin (1960) and Curry et al (1966). Recent work has been carried out by Edwards (1966) and Daley (1969). A complete list of references is given by Edwards (1971). For a description of the Headon Hill section see also sections 3.1 and 3.2.1 of this study.
4.2. Tectonical situation of the type section: Monocline with very low angle dip to the north, which is the extension of the northern limb of the strongly asymmetric E–W trending anticline across the island.
4.3. Contacts of the stratotype with under- and overlying lithostratigraphic units: The Lower Headon Beds rest conformably on marine Barton Beds. The Osborne Beds are overlain by Pleistocene Plateau Gravel.
4.4. Reference to existing geological maps:
   a. Geological Survey of England and Wales – Isle of Wight, New series: parts of sheets 330 and 331, sheets 344 and 345, 1:63360 (1947).
   b. Geological Survey of England and Wales – Lymington (Southampton), sheet 330, 1:63360 (1903).
   c. Geological Survey of England and Wales – Portsmouth (Fareham), sheet 331, 1:63360 (1903).

5. Paleontological description.
5.1. Major fossil groups represented in the stratotype: Pisces, Reptilia, Aves, Mammalia, Mollusca, Ostracoda, Scaphopoda, Foraminifera, nannoplankton, Plantae. For Mammalia see a.o. Lydekker (1885–1887), Cray (1964, 1973), Bosma and Insole (1972), Insole (1972), this study. Many references are found in Cray's and Insole's papers.
5.2. Fossil groups that have been used to correlate the stratotype with other deposits: Mammalia, Mollusca, Ostracoda, Foraminifera, nannoplankton, Plantae. See for references Curry (1966) and Edwards (1971). For correlations by means of Mammalia see Stehlin (1909), Depéret (1917), Cray (1964, 1973), Blondeau et al (1965), Thaler (1966), Franzen (1968), Insole (1972), this paper.
5.3. Rodent zones in the type section: *Isoptychus headonensis* Zone, *Paradelomys quercyi vectisensis* Zone, *Paradelomys quercyi quercyi-Suevosciurus palustris* Zone and probably the *Paradelomys quercyi quercyi-Suevosciurus fraasi* Zone.

5.4. Short ecological analysis: Lacustrine and lagoonal with a single marine ingression in the Middle Headon Beds. See Edwards (1966) and Daley (1969, 1972).

6. Other localities or deposits that are considered to belong to the Headonian:

6.1. On the Isle of Wight the concept of the Headonian is extended in upward direction to include the deposits of the Bembridge Limestone and Bembridge Marls. The only formation that is excluded from the Headonian is the Hamstead Beds. Because it is a poorly exposed unit and so far only comprises one rodent zone (*Eucricetodon atavus* Zone), it is considered better not to erect another stage.
All our localities, except that of Bouldnor Cliff, are considered to be of Headonian Age. In terms of rodent zones also our *Ectropomys exiguus* Zone is incorporated.

6.2. On the basis of biostratigraphical correlation the following localities outside the Isle of Wight should be included in the Headonian: Hordle Cliff (Hampshire, England), Escamps (Quercy, France) as understood in old collections, Ehrenstein 1(A), Weissenburg 8 and Möhren 6 (Fed. Rep. Germany). It is probable, that the localities of Mormont-Eclépens (Switzerland), Neustadt and Nordshausen (Fed. Rep. Germany) and La Débruge (France) also belong to the Headonian.

6.2. Some observations about the position of the Headonian with respect to the classical (marine) chronostratigraphy.

There is considerable uncertainty concerning the chronostratigraphy of the Upper Eocene-Lower Oligocene interval (see Discussions Colloque sur l'Eocène, 1968). Various Upper Eocene stages have been defined, such as Bartonian, Auversian, Marinesian, Ludian and Priabonian, while Lower Oligocene stages include the Latdorfian, Tongrian, Sannoisian and "Conow" Stage (defined by Krutzsch and Lotsch, 1957).

The presence of marine beds in the Isle of Wight sequence makes it possible, to some extent, to correlate with the more or less marine stratotypes on the Continent. Martini and Ritzkowski (1970) suggested correlation between the Upper Barton Beds at Barton Cliff (Hampshire) and the Marnes à *Pholadomya ludensis* (type Ludian) (zone NP 17 of the standard Paleogene calcareous nannoplankton zonation). These authors (1968, 1970) correlated the Brockenhurst Beds (Middle Headon Beds) at Whitecliff Bay with the Upper Priabonian (zone NP 20). Martini (1969) and Martini and Moorkens (1969) considered the Brockenhurst Beds to be older than the type

Latdorfian and the type Lower Tongrian. Any chronostratigraphic evaluation of mammalian faunas based on the original correlation of the Brockenhurst Beds with the type Latdorfian and the type Lower Tongrian seems therefore invalid. The lower part of the Headonian, at least up to and including the middle part of the type section, would be of Eocene age.

In the top part of the continental sequence of the Isle of Wight the Lower Hamstead Beds have been correlated with the Belgian Horizon of Hoogbutsel, since both are considered to contain mammalian faunas of the *Eucricetodon atavus* Zone (see section 5.4). As the Hoogbutsel layers have been situated at the base of the Upper Tongrian, there is little doubt that the Lower Hamstead Beds and the *E. atavus* Zone have to be placed in the Oligocene.

There is no evidence in the correlation towards the marine stages defining the position of the Upper Headon Beds, Osborne Beds, Bembridge Limestone and Bembridge Marls, and of the corresponding zones (two *Paradelomys quercyi quercyi* Zones and the *Ectropomys exiguus* Zone). These sediments and zones, and thus the upper part of the Headonian, seem to straddle the Eocene-Oligocene boundary.

The Latdorfian and Lower Tongrian, which have recently been placed again at the same chronostratigraphic level (Martini and Moorkens, 1969), are commonly considered to represent the lower part of the Oligocene. But over and again the opinion has been expressed that they might just as well, or even might better, be transferred to the Eocene (Marks and Van Vessem, 1971). The Eocene-Oligocene boundary being so obscure in the marine stage succession of north-western Europe, it is self-evident that this limit cannot be sharply pointed at in our rodent zone succession either.

Stehlin's (1909) "grande coupure" is sometimes regarded as a useful level to separate the Eocene from the Oligocene. It may be pointed out that this "limite de premier ordre" occurs between our *Ectropomys exiguus* and *Eucricetodon atavus* Zones.

The contents given to the new stage Headonian is such that it covers a convenient number of zones, starts in the higher Eocene and may eventually appear to have an upper limit at or very close to the Eocene-Oligocene boundary.

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REFERENCES

Blondeau, A., C. Cavelier, L. Feugueur and C. Pomerol (1965). Stratigraphie du Paléogène du bassin de Paris en relation avec les bassins avoisinants, Bull. Soc. Géol. France, (7), *VII*, p. 200–221.

Bonis, L. de (1964). Etude de quelques Mammifères du Ludien de La Débruge (Vaucluse), Ann. Paléontol. (Vertébrés), *L* (2), p. 121–154.

Bosma, A. A. and A. N. Insole (1972). Theridomyinae (Rodentia, Mammalia) from the Osborne Beds (Late Eocene), Isle of Wight, England, Proc. Kon. Ned. Akad. Wet.-Amsterdam, Series B, *75*, no. 2, p. 133–144.

Bosma, A. A. and N. Schmidt-Kittler (1972). *Ectropomys exiguus* n.gen., n.sp., member of the Oltinomyinae n.subfam. (Theridomyidae, Rodentia), from Paleogene deposits of the Isle of Wight (England) and Southern Germany, Proc. Kon. Ned. Akad. Wet.-Amsterdam, Series B, *75*, no. 3, p. 181–192.

Bristow, H. W., C. Reid and A. Strahan (1889). The Geology of the Isle of Wight, Mem. Geol. Surv. (England and Wales).

Butler, P. M. (1972). The problem of insectivore classification, *in* Studies in Vertebrate Evolution, Oliver and Boyd (Edinburgh).

Chatwin, C. P. (1960). The Hampshire Basin and adjoining areas, British reg. Geol. (3rd edition).

Colloque sur l'Eocène, Paris, mai 1968 (1969). Mémoires du B.R.G.M., nos. 58 and 59.

Cray, P. E. (1964). The mammalian fauna of the Headon Beds of Hampshire and the Isle of Wight, Ph.D. Thesis University of Bristol (unpublished).

– (1973). Marsupialia, Insectivora, Primates, Creodonta and Carnivora from the Headon Beds (Upper Eocene) of Southern England, Bull. Br. Mus. nat. Hist. (Geol.), *23*, no. 1.

Curry, D. (1958). Lexique stratigraphique international, Vol. I, fasc. 3aXII, Ed. C.N.R.S.

– (1966). Problems of Correlation in the Anglo-Paris-Belgian Basin, Proc. Geol. Ass., 77, p. 437–467.

–, F. A. Middlemiss and C. W. Wright (1966). The Isle of Wight, Geologists' Association Guide no. 25.

Daley, B. (1969). A palaeoenvironmental study of the Bembridge Marls (Oligocene) of the Isle of Wight, Hampshire, Ph.D. Thesis University of Reading (unpublished).

– (1972). Macroinvertebrate assemblages from the Bembridge Marls (Oligocene) of the Isle of Wight, England, and their environmental significance, Palaeogeography, Palaeoclimatol., Palaeoecol., *11*, p. 11–32.

Dehm, R. (1937). Über die alttertiäre Nagerfamilie Pseudosciuridae und ihre Entwicklung, N. Jahrb. Mineral., Geol., Paläontol., Beil.-Bd.77, Abt.B. p. 268–290.

Denizot, G. (Dir.) (1957). Lexique stratigraphique international, Vol. I, fasc. 4a VII, Ed. C.N.R.S.

Depéret, C. (1917). Monographie de la Faune de Mammifères fossiles du Ludien inférieur d'Euzet-les-Bains (Gard), Ann. Université Lyon, nouv. série, I, 40.

Dixon, W. J. and F. J. Massey, Jr. (1969). Introduction to statistical analysis, Mc Graw-Hill Book Company (3rd edition).

Edwards, N. (1966). A study of the Headon Beds, Osborne Beds and Bembridge Limestone (Upper Bartonian and Lattorfian), in the Isle of Wight and Hampshire, England, Ph.D. Thesis University of Reading (unpublished).

– (1971). Stratigraphy and correlation of the Headon, Osborne, Bembridge, and Hamstead Beds (Palaeogene), Hampshire Basin – a bibliography (1814–1970), J. Soc. Biblphy nat. Hist. *6* (1), p. 50–60.

Forbes, E. (1853). On the fluviomarine Tertiaries of the Isle of Wight, Q.Jl. geol. Soc. Lond., *9*, p. 259–270.

– (1856). On the Tertiary Fluvio-Marine Formation of the Isle of Wight, Mem. Geol. Surv. Great-Britain.

Franzen, J. L. (1968). Revision der Gattung *Palaeotherium* Cuvier, 1804 (Palaeotheriidae, Perissodactyla, Mammalia), Ph.D. Thesis University of Freiburg i. Br.

Gervais, P. (1848–1852). Zoologie et Paléontologie francaises, I, II, III. Bertrand (Paris).

Glibert, M. and J. de Heinzelin (1952). Le gîte des vertébrés Tongriens de Hoogbutsel, Bull. Inst. R. Sci. Nat. Belg., *XXVIII*, no. 52.

Hartenberger, J.-L. (1969). Les Pseudosciuridae (Mammalia, Rodentia) de l'Eocène moyen de Bouxwiller, Egerkingen et Lissieu, Palaeovertebrata, *3* (2), p. 27–61.

– (1971). La systématique des Theridomyoidea (Rodentia), C.R.Acad. Sc. Paris, *273*, série D, p. 1917–1920.

– (1973). Etude systématique des Theridomyoidea (Rodentia) de l'Eocène supérieur, Mém. Soc. Géol. France, no. 117, Nouv. série, t.LII, f. 1–5.

Helmer, D. and M. Vianey-Liaud (1970). Nouveaux gisements de Rongeurs dans l'Oligocène moyen de Provence, C.R. somm. Soc. Géol. France, (2), p. 45–46.

Insole, A. N. (1972). Upper Eocene and Lower Oligocene mammal faunas from southern England, Ph.D. Thesis University of Bristol (unpublished).

Krutzsch, W. and D. Lotsch (1957). Zur stratigraphischen Stellung der Latdorfstufe im Paläogen, Geologie *6* (5), p. 476–501.

Lavocat, R. (1951). Révision de la Faune des Mammifères Oligocènes d'Auvergne et du Velay, Editions "Sciences et Avenir" (Paris).

Lydekker, R. (1885). Catalogue of the fossil Mammalia in the British Museum (Natural History). Part I. Primates, Chiroptera, Insectivora, Carnivora, Rodentia and addendum (London).

– (1885). Part II. Order Ungulata, Suborder Artiodactyla and addenda (London).

– (1886). Part III. The order Ungulata, suborders Perissodactyla, Toxodontia, Condylarthra, Amblypoda, and addenda (London).

– (1887). Part V. The group Tillodonta, the orders Sirenia, Cetacea, Edentata, Marsupialia, Monotremata, and supplement (London).

Major, C. J. Forsyth (1873). Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz, Palaeontographica, *22*, p. 75–130.

Marks, P. and E. J. van Vessem (1971). Foraminifera from the Silberberg Formation ("Lower Oligocene") at Silberberg, near Helmstedt (Germany), Paläont. Z., *45*, 1/2, p. 53–68.

Martini, E. (1969). Nannoplankton aus dem Latdorf (locus typicus) und weltweite Parallelisierungen im oberen Eozän und unteren Oligozän, Seckenbergiana lethaea, *50*, p. 117–159.

– and T. Moorkens (1969). The type-locality of the Sands of Grimmertingen and calcareous nannoplankton from the Lower Tongrian, Bull. Soc. belg. Géol. Paléontol. Hydrol., *78* (2), p. 111–130.

– and S. Ritzkowski (1968). Was ist das "Unter-Oligocän"?, Nachr. Akad. Wiss. Göttingen, II. Math.-Phys. Kl., *13*, p. 1–20.

– and – (1970). Stratigraphische Stellung der obereozänen Sande von Mandrikovka (Ukraine) und Parallelisierungs-Möglichkeiten mit Hilfe des fossilen Nannoplanktons, Newsl. Stratigr., *1* (2), p. 49–60.

Misonne, X. (1957). Mammifères Oligocènes de Hoogbutsel et de Hoeleden. I. Rongeurs et Ongulés, Bull. Inst. R. Sci. Nat. Belg., *XXXIII*, no. 51.

Pomel, A. (1853). Catalogue méthodique et descriptif des Vertébrés fossiles découverts dans le Bassin hydrographique supérieur de la Loire, et surtout dans la vallée de son affluent principal, l'Allier (Paris).

Schlosser, M. (1884). Die Nager des europäischen Tertiärs, Palaeontographica, *31*, p. 19–162.

Schmidt-Kittler, N. (1970). Ein neuer Pseudosciuride von Ehrenstein westlich Ulm, Mitt. Bayer. Staatssamml. Paläont. hist. Geol., *10*, p. 433–440.

– (1971). Odontologische Untersuchungen an Pseudosciuriden (Rodentia, Mammalia) des Alttertiärs, Abh. Bayer. Akad. Wiss., Math.-Nat. Kl., NF, *150*.

Stehlin, H. G. (1909). Remarques sur les faunules de Mammifères des couches Eocènes et Oligocènes du Bassin de Paris, Bull. Soc. Géol. France, 4e série, *IX*, p. 488–520.

– and S. Schaub (1951). Die Trigonodontie der simplicidentaten Nager, Schweiz. Palaeontol. Abh., *67*.

Thaler, L. (1966). Les Rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe, Mém. Mus. Nat. Hist. Nat., série C, Sciences de la Terre, *XVII*.

– (1969). Rongeurs nouveaux de l'Oligocène moyen d'Espagne, Palaeovertebrata, *2* (5), p. 191–207.

Tobien, H. (1971). Mikromammalier aus dem alttertiären Melanienton von Nordhessen, Teil 1: Marsupialia, Insectivora, Primates, Notizbl. hess. L.-Amt Bodenforsch., *99*, p. 9–29.

– (1972). Mikromammalier aus dem alttertiären Melanienton von Nordhessen, Teil 2: Rodentia, Biostratigraphie, Biostratonomie, Notizbl. hess. L.-Amt Bodenforsch., *100*, p. 7–40.

Triat, J.-M., G. Truc and M. Hugueney (1971). Lithostratigraphie des couches d'âge oligocène inférieur et moyen constituant le toit du gypse dans la carrière de Malemort (Vaucluse): données sédimentologiques et paléontologiques, Ann. Université Provence – Sciences, *XLVI*, p. 235–246.

Vianey-Liaud, M. (1969). Rongeurs de l'Oligocène moyen provenant de nouvelles fouilles dans les phosphorites du Quercy, Palaeovertebrata, *2* (5), p. 209–239.

– (1972a). Contribution à l'étude des Cricétidés oligocènes d'Europe occidentale, Palaeovertebrata, *5* (1), p. 1–44.

– (1972b). Un cas de parallélisme intragenérique: l'évolution du genre *Theridomys* (Rodentia, Theridomyidae) à l'Oligocène moyen, C.R. Acad. Sc. Paris, *274*, série D, p. 1007–1010.

– (1972c). L'évolution du genre *Theridomys* à l'Oligocène moyen. Intérêt biostratigraphique, Bull. Mus. Nat. Hist. Nat., 3e série, no. 98, Sciences de la Terre 18.

White, H. J. Osborne (1921). A short account of the Geology of the Isle of Wight, Mem. Geol. Surv. (England and Wales).

Wood, A. E. (1970). The European Eocene Paramyid Rodent, *Plesiarctomys*, Verhandl. Naturf. Ges. Basel, *80*, nr. 2, p. 237–278.

– and R. W. Wilson (1936). A suggested Nomenclature for the cusps of the cheek teeth of Rodents, J. Paleontol., *10* (5), p. 388–391.

PLATE I

Isoptychus headonensis n.sp.

Fig. 1	D_4 sin. (HH1 1).
Fig. 2	P_4 sin. (HH1 11).
Fig. 3	M_{1-2} sin. (HH1 22) (holotype).
Fig. 4	M_{1-2} sin. (HH1 23).
Fig. 5	M_{1-2} sin. (HH1 45).
Fig. 6	M_{1-2} dex. (HH1 34).
Fig. 7	M_3 sin. (HH1 51).
Fig. 8	D^4 dex. (HH1 62).
Fig. 9	P^4 dex. (HH1 73).
Fig. 10	M^{1-2} sin. (HH1 81).
Fig. 11	M^{1-2} sin. (HH1 82).

All figures are x 12.5.

Plate I

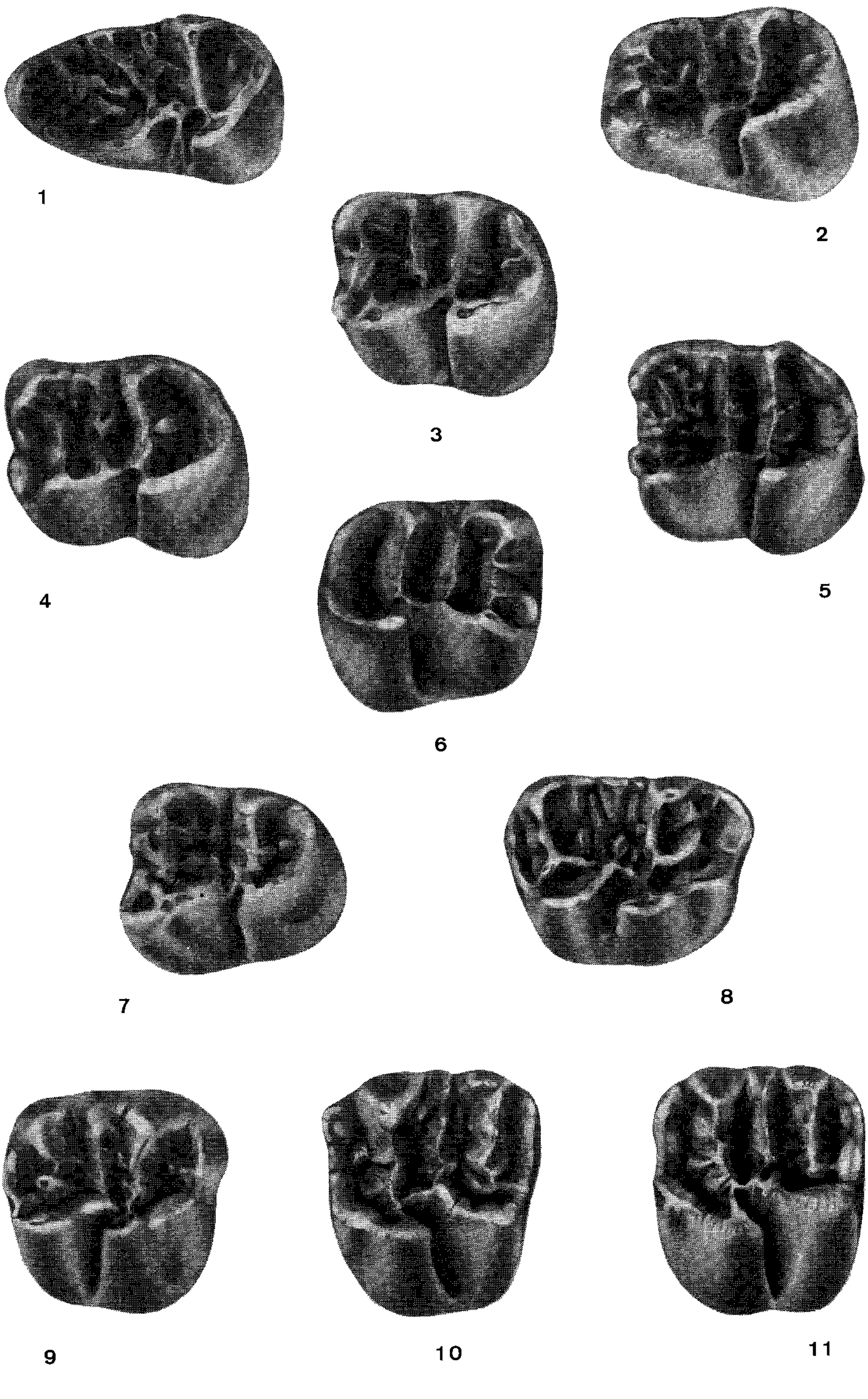


PLATE II

Isoptychus headonensis n.sp.

Fig. 1 M^{1-2} dex. (HH1 93).
Fig. 2 M^{1-2} dex. (HH1 94).
Fig. 3 M^{3} dex. (HH1 113).
Fig. 4 Fragment of left upper jaw with P^{4}-M^{2} (B.M.(N.H.) 30159a6).

Isoptychus pseudosiderolithicus De Bonis, 1964

Fig. 5 Fragment of left upper jaw with P^{4}-M^{1} (WB2B 1).
Fig. 6 M_{1-2} dex. (HH2 711).
Fig. 7 D^{4} dex. (HH2 731).
Fig. 8 P^{4} dex. (HH2 741).
Fig. 9 M^{1-2} dex. (HH2 762).
Fig. 10 M^{3} dex. (HH2 771).

Figures 1–3 and 6–10 are x 12.5, figures 4–5 are x 6.

Plate II

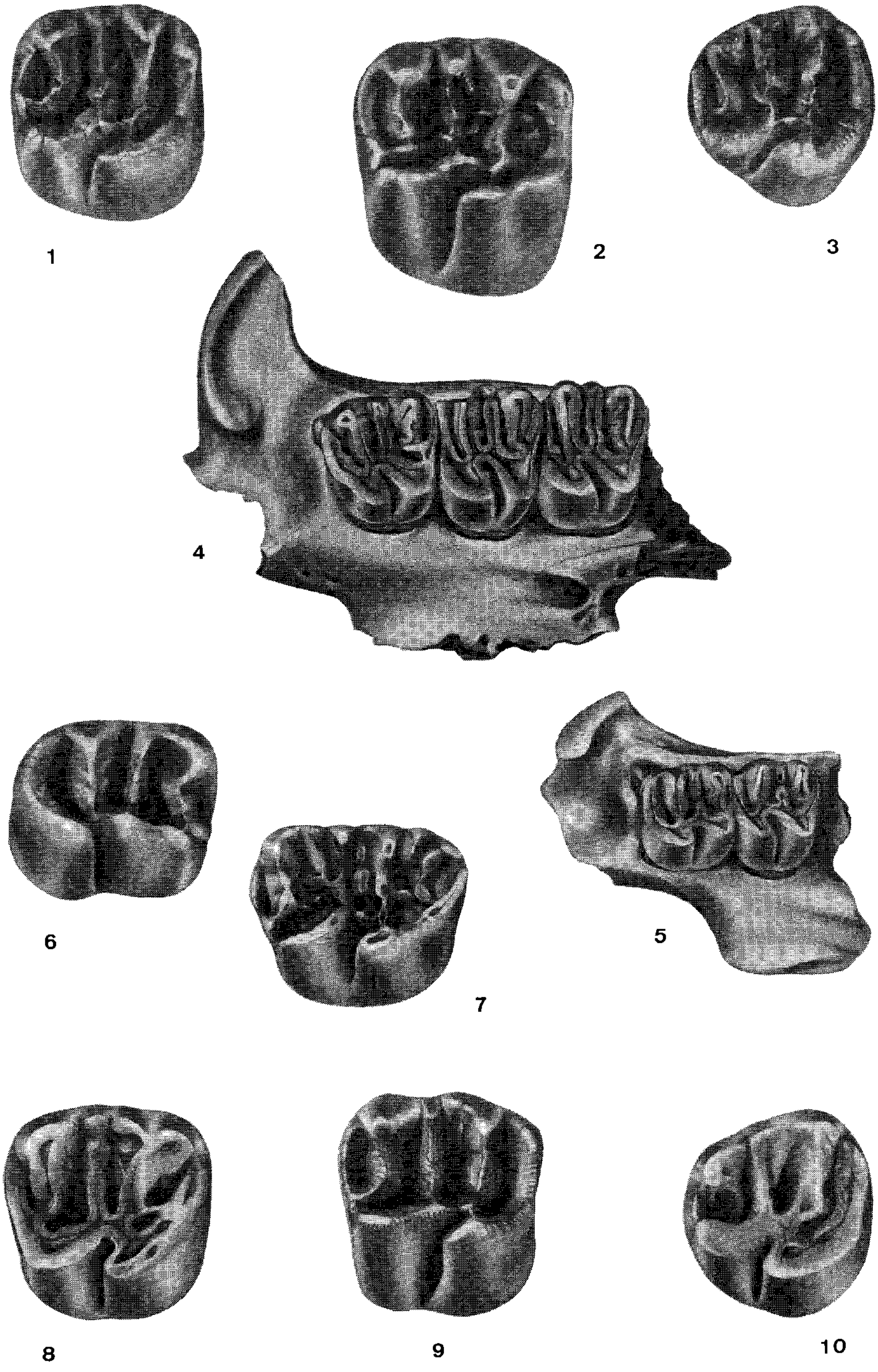


PLATE III

Isoptychus pseudosiderolithicus De Bonis, 1964

Fig. 1	D_4 sin. (F.C. BC(FD) 1).
Fig. 2	P_4 sin. (F.C. BC(FD) 34).
Fig. 3	$M_{1\text{-}2}$ dex. (F.C. BC(FD) 131).
Fig. 4	$M_{1\text{-}2}$ dex. (F.C. BC(FD) 157).
Fig. 5	M_3 sin. (F.C. BC(FD) 303).
Fig. 6	M_3 sin. (F.C. BC(FD) 301).
Fig. 7	D^4 sin. (F.C. BC(FD) 361).
Fig. 8	P^4 sin. (F.C. BC(FD) 453).
Fig. 9	$M^{1\text{-}2}$ sin. (F.C. BC(FD) 513).
Fig. 10	M^3 sin. (F.C. BC(FD) 722).
Fig. 11	M^3 sin. (F.C. BC(FD) 728).

Paradelomys quercyi quercyi (Schlosser, 1884)

Fig. 12 Fragment of right upper jaw with P^4-M^1 (B.S.P.G. 1879 XV-541).

Figures 1–11 are x 12.5, figure 12 is x 6.

Plate III

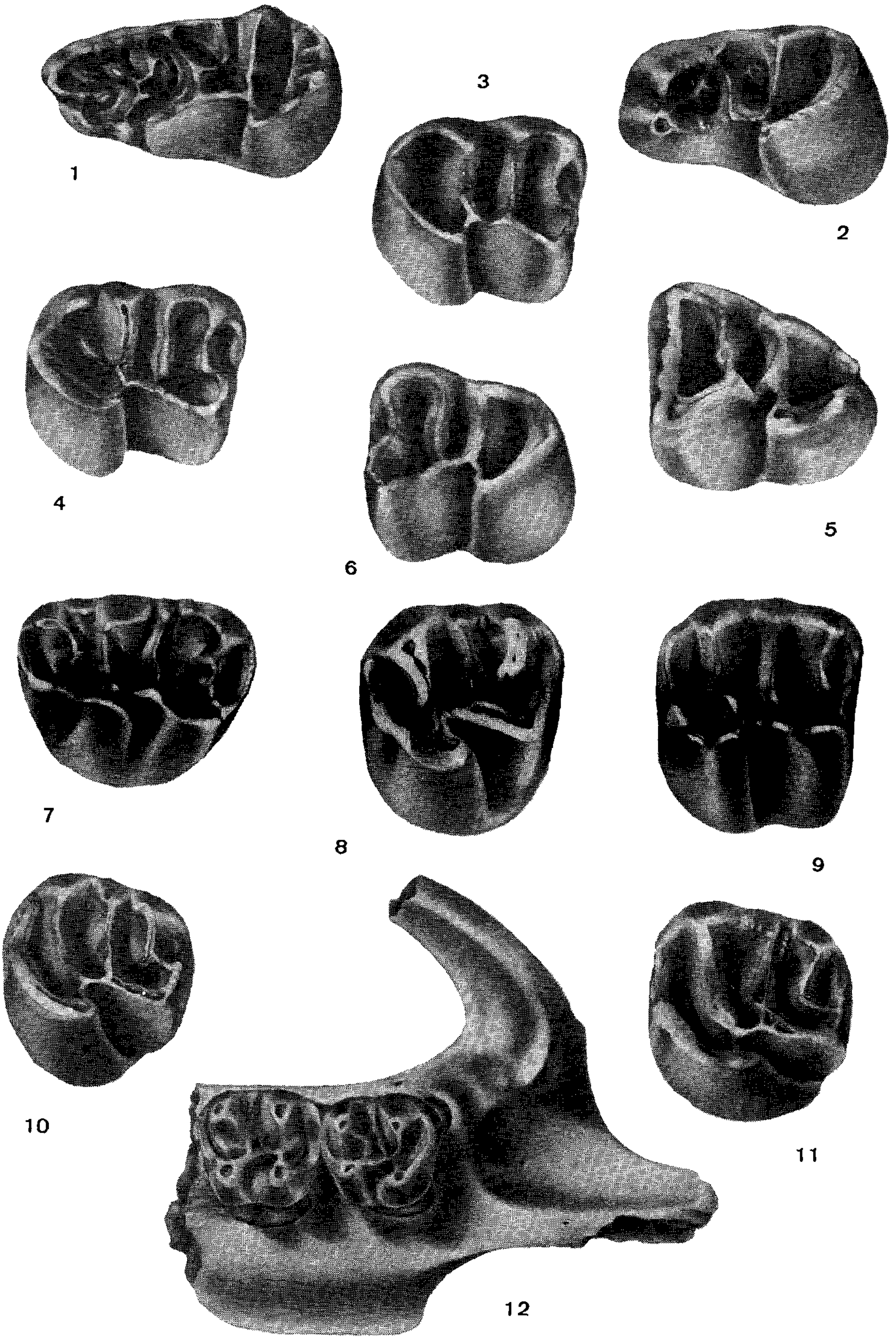


PLATE IV

Steneofiber sp.

Figs. 1a-b Fragment of left lower jaw with P_4-M_1 (B.M.(N.H.) M14748).

Fig. 2 P_4 sin. (B.M.(N.H.) M19207).

Pseudoltinomys gaillardi (Stehlin and Schaub, 1951)

Fig. 3 P_4 dex. (F.C. BC(FD) 1302).

Fig. 4 M_{1-2} sin. (F.C. BC(FD) 1304).

Fig. 5 M_3 dex. (F.C. BC(FD) 1312).

Fig. 6 D^4 dex. (F.C. BC(FD) 1315).

Fig. 7 P^4 sin. (F.C. BC(FD) 1316).

Eucricetodon atavus (Misonne, 1957)

Fig. 8 M^1 dex. (F.C. BC(FD) 1201).

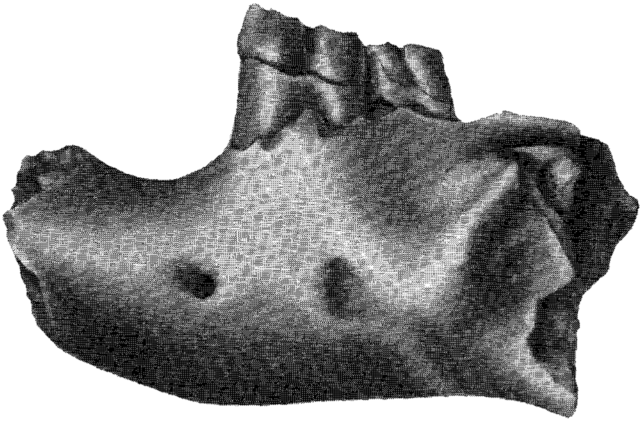
Fig. 9 M^2 sin. (F.C. BC(FD) 1211).

Plesiarctomys sp.

Fig. 10 M^{1-2} sin. (F.C. HH1(FD) 1).

Figures 3–10 are x 12.5, figures 1b and 2 are x 6, figure 1a is x 3.

Plate IV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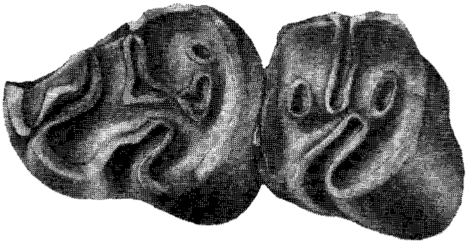
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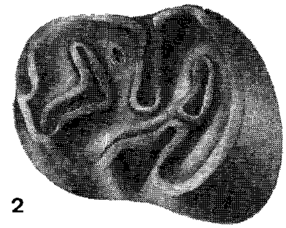
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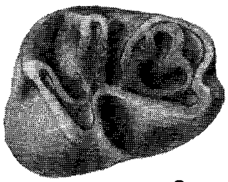
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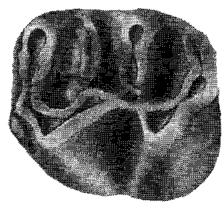
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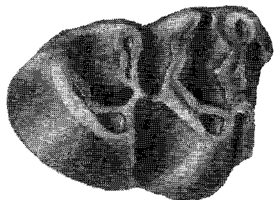
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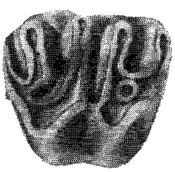
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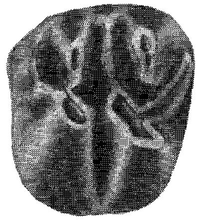
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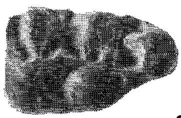
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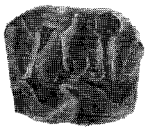
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10

PLATE V

Sciuroides ehrensteinensis Schmidt-Kittler, 1971

Fig. 1 M_{1-2} dex. (F.C. HH2(FD) 1).

Fig. 2 M_{1-2} sin. (HH 401).

Fig. 3 M_3 sin. (HH3 751).

Fig. 4 D^4 sin. (HH2 1051).

Fig. 5 M^{1-2} dex. (HH1 141).

Fig. 6 M^{1-2} sin. (HH2 1062).

Suevosciurus palustris (Misonne, 1957)

Fig. 7 M_{1-2} sin. (HH3 412).

Fig. 8 M_{1-2} sin. (TB 424).

Fig. 9 M^{1-2} sin. (HH3 463).

All figures are x 12.5.

The figures on plates IV (figs. 8–10) and V–VII are based on photographs made with a "S4 Stereoscan" Scanning electron microscope on Ilford FP4 black and white panchromatic safety films.

Plate V

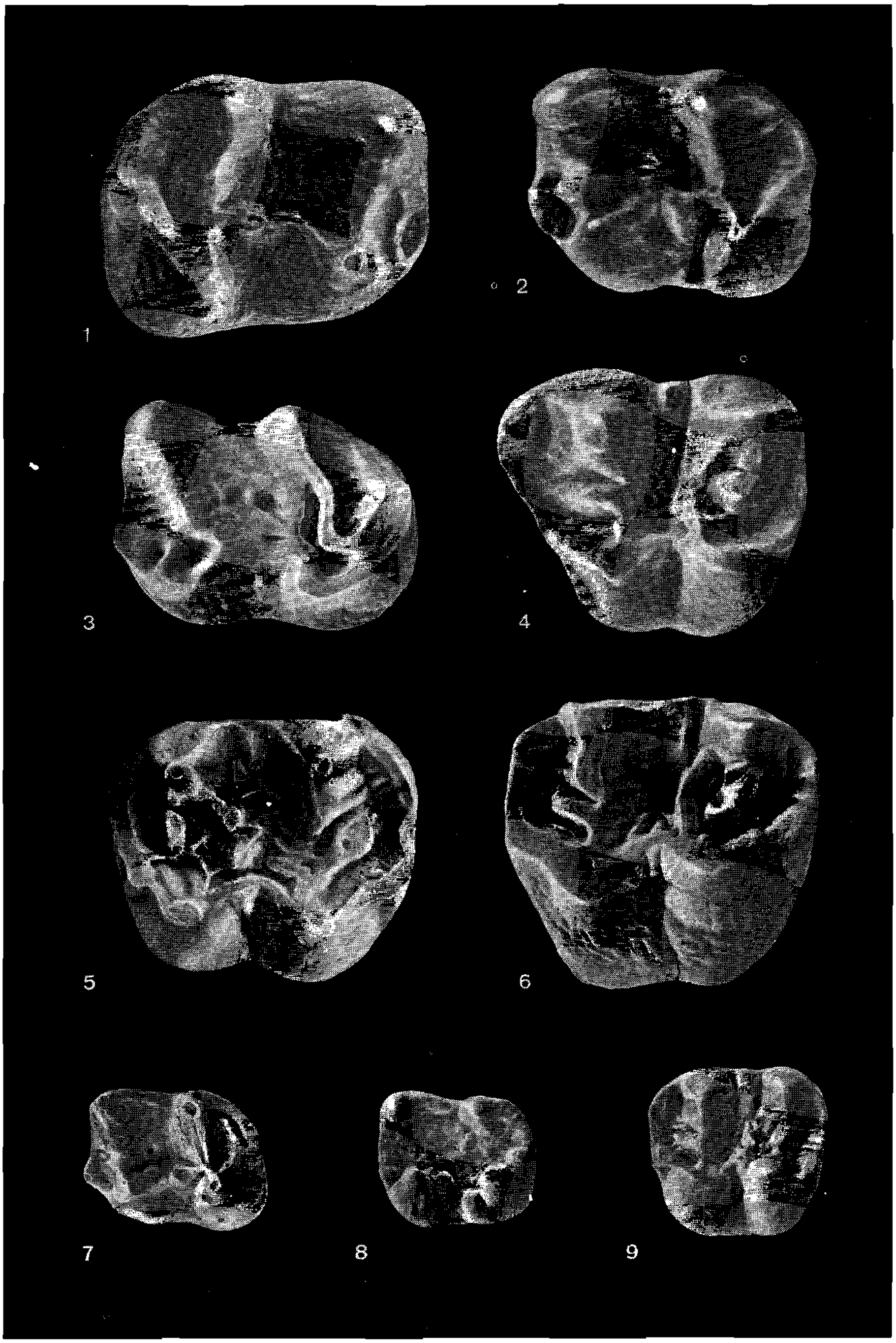


PLATE VI

Treposciurus mutabilis helveticus Schmidt-Kittler, 1971

Fig. 1 P_4 sin. (HH2 1091).

Fig. 2 D^4 sin. (HH3 572).

Treposciurus intermedius (Schlosser, 1884)

Fig. 3 M_3 dex. (HH2 1251).

Fig. 4 D^4 dex. (F.C. WB2A(FD) 22).

Fig. 5 P^4 dex. (HH 421).

Fig. 6 P^4 sin. (F.C. WB2A(FD) 23).

Fig. 7 M^{1-2} dex. (HH1 182).

Fig. 8 M^{1-2} dex. (F.C. WB2A(FD) 24).

Fig. 9 M^{1-2} sin. (WB2A 601).

Fig. 10 M^3 dex. (F.C. WB2A(FD) 26).

All figures are x 12.5.

Plate VI

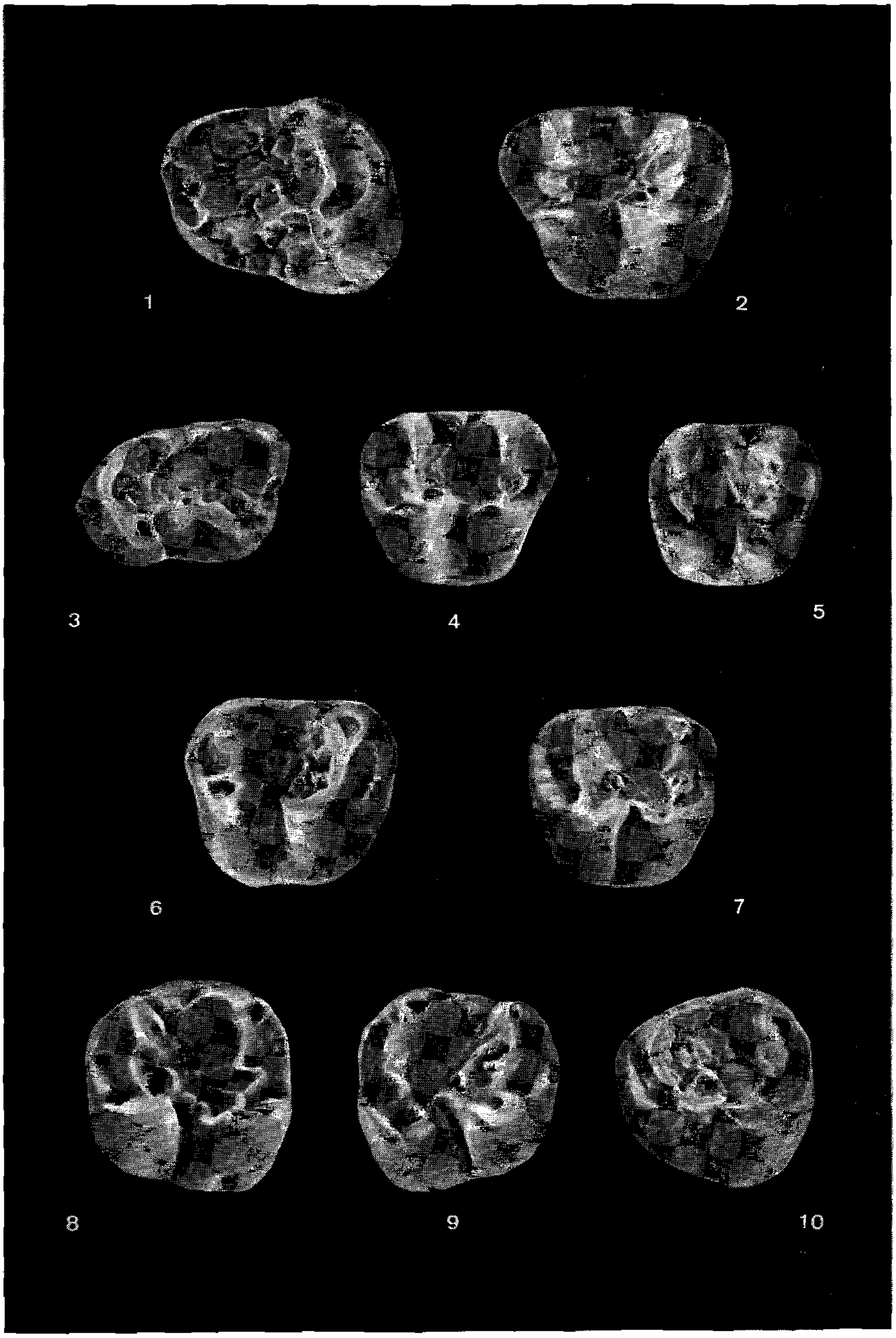


PLATE VII

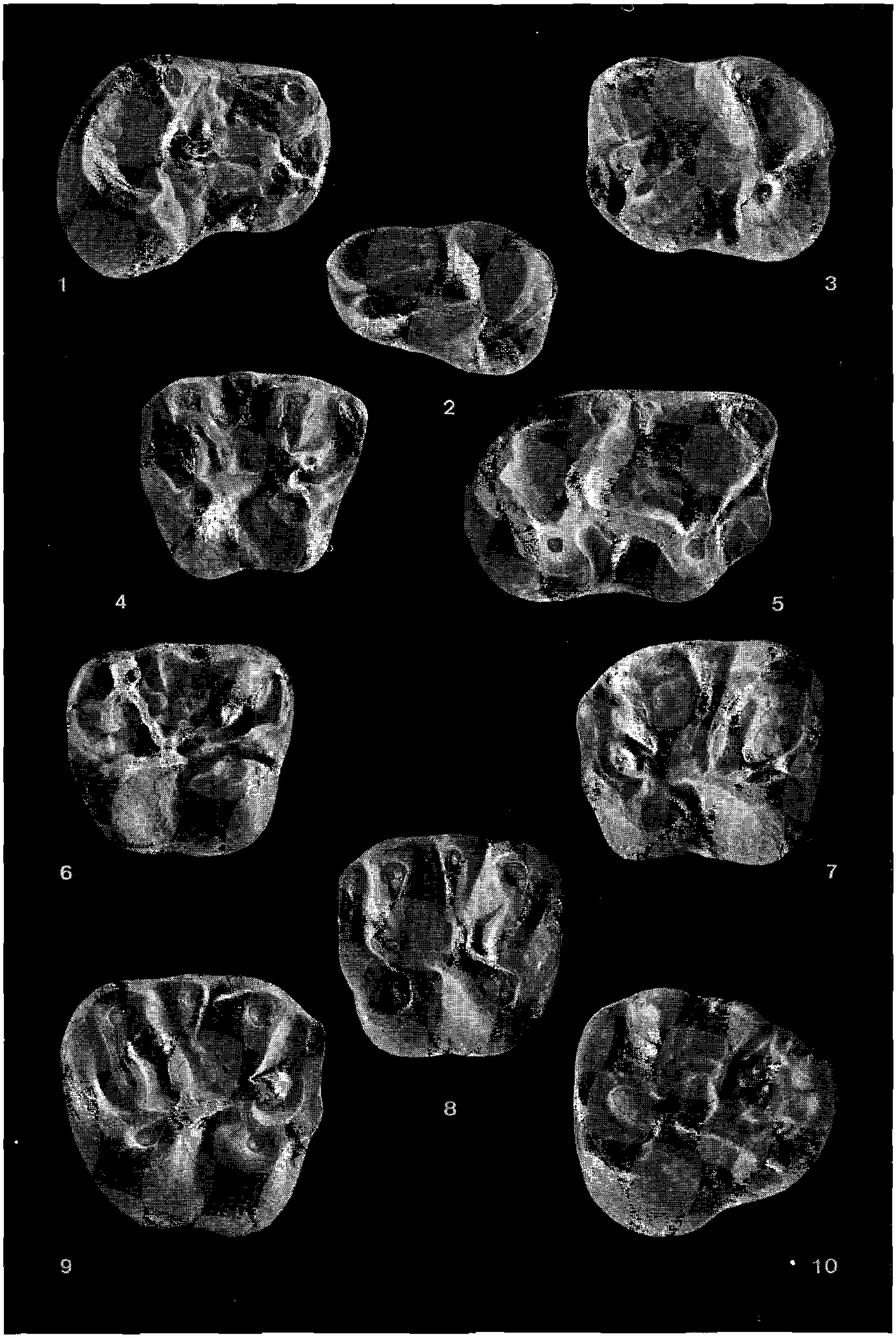
Paradelomys quercyi quercyi (Schlosser, 1884)

Fig. 1 P_4 dex. (HH3 651).
Fig. 2 D_4 sin. (HH4 301).
Fig. 4 D^4 dex. (HH3 682).
Fig. 5 M_3 dex. (HH3 671).
Fig. 6 P^4 dex. (HH3 691).
Fig. 7 M^{1-2} sin. (HH4 315).
Fig. 9 M^{1-2} dex. (HH4 314).
Fig. 10 M^3 sin. (HH3 711).

Paradelomys quercyi vectisensis n.subsp.

Fig. 3 M_{1-2} sin. (HH2 1181).
Fig. 8 M^{1-2} sin. (HH2 1221) (holotype).

All figures are x 12.5.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SAMENVATTING

In dit proefschrift worden de taxonomie en stratigrafische bruikbaarheid van knaagdieren uit de Boven Eocene en Onder Oligocene afzettingen van het eiland Wight behandeld.

Het taxonomische deel bevat beschrijvingen van soorten behorende tot de families Pseudosciuridae, Theridomyidae, Cricetidae, Castoridae en Paramyidae. Eén van deze soorten is nieuw, een andere soort wordt verdeeld in twee ondersoorten. De inhoud van de verschillende taxa wordt aan een kritische beschouwing onderworpen.

In het biostratigrafische deel wordt op grond van de vertikale verspreiding van de soorten een zestal "range zones" en "concurrent range zones" onderscheiden: de *Isoptychus headonensis* Zone, de *Paradelomys quercyi vectisensis* Zone, de *Paradelomys quercyi quercyi-Suevosciurus palustris* Zone, de *Paradelomys quercyi quercyi-Suevosciurus fraasi* Zone, de *Ectropomys exiguus* Zone en de *Eucricetodon atavus* Zone.

In het chronostratigrafische deel wordt een nieuwe etage in de chronostratigrafische schaal voor continentale afzettingen voorgesteld. Deze nieuwe etage, het Headonien, lijkt gecorreleerd te kunnen worden met delen van het Priabonien en Onder Tongrien van de chronostratigrafische schaal van de mariene afzettingen.

CURRICULUM VITAE

Toegevoegd op verzoek van het college van dekanen der Rijksuniversiteit te Utrecht.

De schrijfster van dit proefschrift behaalde in 1961 het diploma H.B.S.-B aan de toenmalige Rijkshogereburgerschool te Leeuwarden. In hetzelfde jaar begon zij met de studie in de biologie aan de Rijksuniversiteit te Utrecht. In juni 1966 legde zij het kandidaatsexamen af, in september 1968 het doktoraalexamen (hoofdvak erfelijkheidsleer, bijvakken paleozoölogie en fysiologie van de mens). In februari 1969 maakte zij een aanvang met haar promotie-onderzoek.

Van november 1969 tot juni 1970 was zij als doktoraal-assistente c.q. wetenschappelijk medewerkster part-time werkzaam bij het Instituut voor Antropobiologie van de Rijksuniversiteit te Utrecht. Gedurende het jaar 1972 was zij in dienst van de Nederlandse organisatie voor zuiver-wetenschappelijk onderzoek. Vanaf 1 januari 1973 is zij als wetenschappelijk medewerkster verbonden aan de vakgroep Funktionele Morfologie van de Fakulteit der Diergeneeskunde.